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THE BOTANICAL GAZETTE

Editor: JOHN M. COULTER

SEPTEMBER 1922

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THE BOTANICAL GAZETTE

A MONTHLY JOURNAL EMBRACING ALL DEPARTMENTS OF BOTANICAL SCIENCE

EDITED BY

JOHN M. COULTER

With the assistance of other members of the botanical staff of the University of Chicago

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VOLUME LXXIV NUMBER 1

THE
BOTANICAL GAZETTE

September 1922

DEVELOPMENT OF PLANT COMMUNITIES OF A SAND RIDGE REGION IN MICHIGAN

W. G. WATERMAN

(WITH TWELVE FIGURES)

Plant synecology is the study of the relations of plant communities to their environment. The subject may be divided into three major sections.

1. *Morphological and physiological synecology.*—The physiognomy, ecological structure, and floristic composition of plant communities and their relationship to the factors of the environment. This includes not merely an enumeration of the species and ecological forms present, but also the sociological value of the different members of the community, as suggested in the following topics: abundance, dominance, affiliation, genetic importance, constancy, etc.

2. *Geographic synecology.*—The distribution of plant communities, with special reference to the influence of the factors of environment.

3. *Genetic or dynamic synecology.*—The study of the development of plant communities on unit areas as the result of the action of biotic factors, modified by physiographic influences and by changes of climate.

In the early days of ecology, the distributional phase of synecology was more evident and was followed with almost no suggestion

of the others. In recent years the other phases have been increasingly studied, but all have generally been combined in a more or less haphazard fashion. In a geographically extended treatment of the subject, the distributional (geographic) division may either precede or follow the developmental (genetic) division. If the communities are considered merely from the standpoint of their floristic content, their distribution may be studied first, and this has been the historical order. Plant geography has been studied with increasing interest since the days of VON HUMBOLDT, and it is still an important branch of synecology. It is evident, however, that the distribution of communities identified and named in accordance with their position in a developmental series (associations, formations, etc.) cannot be carried out adequately until a genetical study of those communities has been completed. In a limited area the study of the distribution of communities is correspondingly limited, and is of value only as it helps to determine the developmental relationships of these communities.

As genetic synecology is the most recent branch of the subject, and its content is not yet fully organized, a brief historical statement will be in order at this point. COWLES (3) was the first to form a comprehensive system based on the dynamic element in plant communities, as a result of his difficulty in classifying the communities of the Chicago region in accordance with WARMING'S principles. He was so strongly impressed with the influence of the physiographic factors that he outlined his system on that basis. Later (4) he recognized climatic, physiographic, and biotic factors as the three great causes of plant succession.

CLEMENTS (1) pointed out that climatic and physiographic causes produce succession but not true development, that is, the building up of a quasi-organism; and that this was possible only by the action of biotic factors, and especially by the influence of the plants which compose the different communities. CLEMENTS bases his main divisions on his climaxes or "formations," his next division is into primary and secondary successions, and his third into hydrosere and xerosere, based on the water content of the initial area. For these divisions he also uses as adjective modifiers the term hydrarch and xerarch, suggested by COOPER (2). As these

latter refer especially to the beginning of the succession, they are more suitable in this connection than such terms as hydrosere, etc., which apply to the moisture content of the whole succession, because in most cases the initial moisture condition does not persist, and the substratum generally approaches a mesophytic condition. While this classification may be logically defensible, CLEMENTS does not give sufficient consideration to the fact that the actual lines of development are determined by the nature of the substratum, that the floristic content of the pioneer stages is absolutely different in clay, sand, or rock, and that it is only as the seres approach the climax stage that they begin to converge and to resemble each other. Furthermore, standing water should be regarded as a type of substratum, because its pioneer stages are practically identical in ponds on rock, sand, or clay, and are quite different from the pioneer stages of wet sand or clay, to which stages the term hydrarch should be restricted. The subdivisions of the primary succession (prisere), therefore, should be sand succession (psammosere), clay succession (geosere), rock succession (lithosere), and aquatic succession (hydrosere). The first three successions have wet and dry initial stages (hydrarch, xerarch). It is evident that this classification does not distinguish the many types of substratum containing mixed sand, clay, and gravel. It does not seem, however, that these are sufficiently well marked or sufficiently different as to vegetation to warrant establishing one or more additional seres for them at present.

The terminology of the units of genetic synecology is being much discussed at present. It is generally agreed that the fundamental unit in the developmental classification of communities is the association. At first this was defined in terms of the habitat, but in 1921 NICHOLS (**7**), as a result of several questionnaires sent to eighty-five ecologists, reported at the recent meeting of the Ecological Society of America at Toronto that a large majority of the ecologists consulted favored the following statements: (1) That the term plant association be recognized as applicable both to the abstract vegetation concept and to the concrete individual pieces of vegetation upon which this concept is based; (2) that plant association in the abstract be defined somewhat as follows: an ecological vegetation-

unit characterized by an essentially definite physiognomy and ecological structure, and by an essentially definite floristic composition as regards dominant species; (3) that plant association in the concrete be defined somewhat as follows: a plant community of essentially uniform (or homogeneous) physiognomy and ecological structure and of essentially uniform (or homogeneous) floristic composition as regards dominant species. This simply formulates the more or less unconscious practice of most ecologists, who, when speaking of "a *Scirpus-Typha* association" have a concrete community in mind, while "the *Scirpus-Typha* association" of a certain region is plainly an abstract concept.

The next higher unit is also generally recognized as the formation, but there is not yet the same agreement in regard to its content as there seems to be for the association. The following brief survey of the progress of opinion in regard to the formation is summarized from TANSLEY (9). According to the definition adopted by the Brussels Congress, the formation is composed of associations which differ in their floristic composition, but are in agreement (1) with the conditions of the habitat, and (2) as regards their growth forms. TANSLEY says, "Though this concept is apparently accepted by most European phytogeographers, it has little real hold on actual concrete research because it is abstract and one sided." In 1907 MOSS (5) proposed a unit, later embodied by TANSLEY (8), in which all associations developed on the same habitat or on one of essentially constant character were considered as belonging to one formation. Not all the stages of a succession were necessarily included in one formation. If the habitat obviously changed its character completely, it was recognized that a new formation had been initiated. This conception was widely criticized, and TANSLEY admitted the validity of criticisms of the habitat element in the definition. CLEMENTS (1) refused to recognize any formations except those determined by climate, regarding all communities in a region where forests are climatically possible only as stages in the development of forest formations. TANSLEY believes that this view has not been generally accepted in Europe or in America, and feels that the universal dominance of climatic factors as determinants of climax vegetation has not been proved.

NICHOLS (6) recognized this and returned to SCHIMPER's distinction between climatic and edaphic formations. His unit next above the association was the edaphic, later called the physiographic formation, which he defined as the association-complex occupying a physiographic unit area, while the climatic formation was a complex of physiographic formations forming the vegetation, taken in its entirety, of any region in which the essential climatic relations are similar or uniform throughout. This TANSLEY criticized, because "nothing like a sharp line can be drawn between one climatic region and another, so that it becomes impossible to delimit climatic formations in NICHOLS' sense." TANSLEY accepts CLEMENTS' "associes" for all stages which have not reached a relatively stable (climax) condition, and defines the association as a mature quasi-organism which is relatively fixed and stable. He then defines the formation as including "all the vegetation which is naturally grouped around the association, determined by the particular collection of environmental factors which make up the ecological conception of the habitat." NICHOLS has not published as yet any further statement on the formation, but in his paper at the Toronto meeting he seems to adhere to his division of formations as physiographic and climatic.

As a result of a study of literature on formations, as well as actual conditions in the field, especially in connection with the preparation of the present paper, the writer has reached the following conclusions, on which the definitions of the terms involved will be based.

1. That there is a distinct advantage in omitting from the definition of the formation all reference to the habitat, as was done in the case of the association.

2. That it is inadvisable to connect the idea of the formation with a climax association, because the determination of climax is one of the purposes of a genetical study, and it is clearly undesirable to define a term which should be usable from the beginning of a study in such a way that it cannot properly be used until the study has been completed. In such a case it would be necessary to secure an additional term for the community in the process of development. This is cumbersome and unsatisfactory, as is illustrated in CLEMENTS' use of "associes" and "association," which does not

seem to meet with general approval in this country at least. In this case there is the additional objection that the more familiar and convenient term is restricted in use to a minority of cases.

3. That the double aspect, abstract and concrete, approved for the association be recognized also for the formation. The abstract concept of the formation, indicated by the use of the definite article, would thus correspond with the Brussels Congress description, and would constitute the formation abstract as a sort of ecological species. The formation concrete might then be regarded simply as any association complex, characterized by a dominant association but including all adjacent associations, whether mature or immature, and other more or less anomalous or unidentified communities connected with them. Thus the formation concrete in general would correspond to NICHOLS' physiographic formation, although the habitat is omitted from the definition, and contiguity made the basis on which the communities are united in the formation. Individual formations may be named either from the dominant association or from the physiographic nature of the area occupied.

4. If a unit above the formation is desired, it will be found convenient to associate the formations of a region in a larger group, which NICHOLS (**6**), following SCHIMPER, has characterized as a climatic formation. TANSLEY has demonstrated the inadvisability of the term, but the fact remains that the concept is a convenient one, especially for field use, and the writer suggests that the term "formation complex," or simply "complex," be used for this concept. If it be objected that complex is equally applicable to lower grades of units, and is actually in use with them, a special term, such as "aggregate," might be employed. It does not seem advisable to use the term formation, even if qualified by a descriptive adjective, for two classes of units of different grade. Indeed this concept may be identified sufficiently by general expressions already in use, such as vegetation, formations, or even forest (as in "vegetation of Connecticut," "formations of the Great Lakes region," "temperate deciduous forest," etc.).

On the whole, it seems advisable to follow TANSLEY and NICHOLS in emphasizing the vegetational content of the community and regarding the habitat as the sum total of the environmental factors,

and therefore not employing it to indicate any definite portion of the surface of the earth. There is an advantage in employing a special term for the ground occupied by each synecological unit, and the writer tentatively uses the word "locality" for the ground occupied by an individual association, "area" [1] for that occupied by a formation, and "region" for that occupied by a formation complex.

The present study is to be regarded as a preliminary reconnoissance rather than as a completed work. Its purpose is to indicate the lines along which such a study should proceed, and to suggest some tentative conclusions. It is the intention of the writer to make a thorough study of the morphology and physiology of these communities, and in the light of those results to review the tentative conclusions now reached. This preliminary survey will also serve to introduce the region to ecologists, and to show the unusual opportunity for the study of the very diverse communities of a region in relatively primitive condition. Incidentally the writer regards the region as one which should be included in a list of regions to be preserved in their natural condition.

Description of habitat

GEOGRAPHY.—The region is located in Benzie County, Michigan, and adjoins on the north the Crystal Lake Bar region already reported (10). It may be described as a right-angled triangle whose base is about eight miles long, extending south-southeast from a point on the shore of Lake Michigan about two miles northeast of Point Betsie, almost to the town of Honor on Platte River. The east side of the region is the perpendicular of the triangle, and extends north from Honor nearly to the town of Empire on Lake Michigan. The shore forms the hypothenuse, curving slightly to the south with a projection at the mouth of Platte River. It has a total area of about twenty-five square miles, of which perhaps one-fifth is occupied by lakes and ponds. The region is locally known as the Platte Plains, although it is composed of sand ridges and hills, and the general relief is distinctly rolling rather than flat (fig. 1).

The Lake Michigan shore is bordered by a strip of moving dunes ranging from 200 to 500 yards wide. As the prevailing winds are

[1] This is an ecological use of the term, and differs materially from its floristic use.

from the southwest, this dune strip has been protected by the morainic ridge (fig. 2) north of Point Betsie, and the dunes are relatively low and do not have the scenic features to be found in similar areas elsewhere. South of the narrow belt of moving dunes are found the sand ridges, roughly parallel with the shore, with intervening depressions, some still containing small ponds. These ponds occur almost exclusively in the portion of the region west of Platte

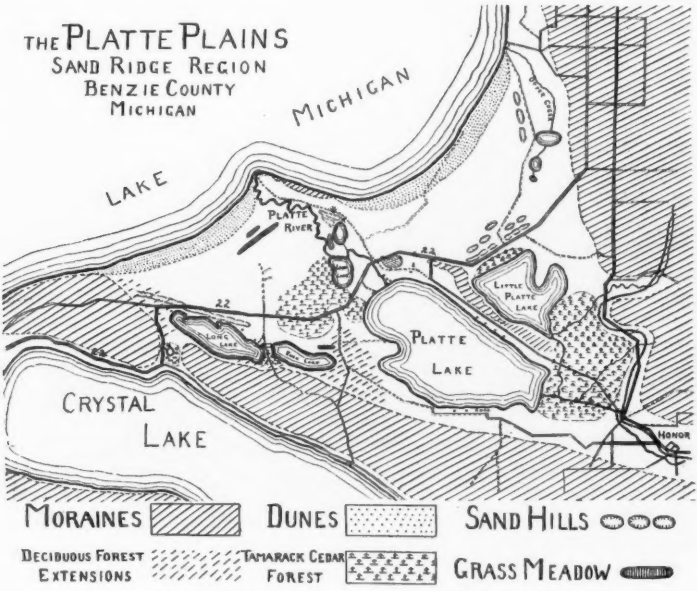

FIG. 1.—Map of Platte Plains sand ridge region

River, probably because of the protection of the morainic ridge which has prevented them from being filled by blown sand. Between the sand ridges lies a wide trough of relatively slight depth, which contains a series of six lakes, more or less completely connected and draining into the Platte River, and three small lakes draining to the north through Otter Creek.

GEOLOGY.—This region is regarded as having been a shallow embayment of Lake Algonquin, whose shores were formed by

morainic uplands. The shore line of the embayment is clearly traceable along the southern and eastern border of the Platte Plains as shown on the map. On the west the old shore line, protected by the morainic ridge, is marked by low rounded knolls, but on the south and east it still shows the characteristics of a wave-formed bluff (fig. 3). This feature has been continued by wave action in the lakes on the south, and it is especially marked on the east, where it borders the floodplain of Otter Creek (fig. 7). There it still remains as a steep bank rising 150 or 200 feet above the plains. The present

FIG. 2.—View toward southwest over shore dunes to morainic ridge which formed the Algonquin shore on the south.

sand ridges with intervening depressions were formed originally as sand bars by the receding waters of Lake Algonquin, assisted by the winds, which piled dunes of varying heights up to 100 feet above Lake Michigan on the successive beaches left bare by the receding lake. One morainic fragment is found on the present shore line half a mile east of the mouth of Platte River, in shape like a hogback, with a very steep forested slope on the south and an equally steep bluff of erosion facing the lake (fig. 10). The line of hills between Platte Lake and Little Platte is a morainic remnant exactly in line with the fragment on the shore. Morainic gravel has been found

in at least one spot midway between the two; so it seems probable that these represent the remains of a moraine which originally bisected the triangle, and which later determined the location of Platte River.

ENVIRONMENTAL CONDITIONS.—The factors of the environment are similar to those of the Crystal Lake Bar region (10), and will not be repeated here. A study of the soil acidity by WHERRY'S method is planned for the near future, and will probably yield interesting results. The variations in soil and moisture content are evidently

FIG. 3.—View toward the southwest over Platte Lakes, showing Algonquin shore line in distance.

of great importance. The substratum consists in the main of beach and dune sand, but there is a mixture of morainic material around the edges where moraine clay and gravel were washed down by the waves of Lake Algonquin and by atmospheric agencies since that time. The materials of the low morainic ridge which bisect the area are also of considerable importance, and their significance will be considered in connection with the migration of the deciduous forest elements into the sand ridge vegetation.

While the slight moisture content of the superficial layer of sandy soil is generally recognized, it has been thought that the

moister conditions of lower layers and the low wilting coefficient of sand would prevent a serious deficiency of moisture for plants adapted to that habitat. The very dry weather in the first part of the summer of 1921, however, apparently caused serious results, although the full effects of these conditions cannot yet be determined. The leaves of the blueberries and other small shrubs dried up early, and while the plants were not killed, their vegetative development for the following summer was greatly reduced. A number of oak and pine seedlings up to two feet in height were evidently killed.

FIG. 4.—Typical sand ridge vegetation, with *Pteris aquilina* in center

Similar "red summers" were reported by the farmers as having occurred at intervals of eight or ten years. It is evident that they would profoundly affect the development of a dense growth of trees on these ridges. Various fires, chiefly prehistoric, have also had an influence. The areas which were affected by these fires should be determined and mapped, and their influence on the present vegetation more definitely determined.

Morphology and distribution of communities

MOVING DUNE FORMATION.—The dune vegetation is practically the same as that of the Point Betsie dune complex already described

(10, 11), with the important exception that there are numerous groves of *Pinus Banksiana* occupying depressions just back of the foredune, and apparently originating in pannes.

SAND RIDGE FORMATION.—The sand ridge area was originally covered by a forest of pine and oak whose trees had reached considerable size. This forest had been burned before the white settlers came to the region. Many of the dead trees were cut while still standing, and many of their stumps still remain. A few patches were not burned, perhaps being protected by neighboring bodies of water, and these give some idea of what the original forest might have been (fig. 8). Reproduction has been good all over the region, and with fifty years' growth behind it, the forest might be regarded as half-way to maturity. While strictly this region should be regarded as a secondary succession, most of the area has practically been untouched by man, and the development seems to be well on its way toward a reproduction of its original condition, so that with the aid of apparently untouched portions it should be possible to work out the stages of the original succession.

The trees of this formation in the order of their importance are *Pinus Strobus*, *P. resinosa*, *P. Banksiana*, *Quercus ellipsoidalis*, *Q. alba*, *Q. rubra* (*Q. velutina* apparently should belong here, but has not been certainly identified), *Acer rubrum*, *Betula alba papyrifera*, *Populus tremuloides*, *P. grandidentata*, *Amelanchier canadensis*, and *Prunus pennsylvanica*. The shrubs found on the sand ridges are *Cornus stolonifera* near the dune belt and *Rhus typhina* farther south (fig. 4). In the undergrowth are found *Pteris aquilina*, *Gaultheria procumbens*, *Vaccinium vacillans*, *V. pennsylvanicum*, *Melampyrum americanum*, and *Ceanothus virginiana*, with *Cladonia rangiferina*, several cushion mosses, and occasionally *Selaginella rupestris* in the drier portions. In the more mesophytic spots occur also *Pedicularis canadensis*, *Galium* sp., *Maianthemum canadense*, *Diervilla Diervilla*, and *Aster cordifolius*. Near the dunes are found *Artemisia canadensis*, *Smilacina stellata*, *Arctostaphylos uva-ursi*, *Apocynum cannabinum*, *Rosa blanda*, *Juniperus communis*, and *J. horizontalis*.

ASSOCIATIONS OF SAND RIDGE DEPRESSIONS.—The depressions between sand ridges are small oval bowls or pockets averaging only a few hundred yards in greatest length. They show all types of

aquatic communities, from those which are nearly all floating aquatics to the grass meadow or the swamp shrub thicket. There are few characterized by a true bog mat, but many contain characteristic bog plants and shrubs. The grass meadows vary in size from a few yards in diameter to one 100 yards wide, and one-half to three-quarters of a mile long; while two others of equal length are 200–300 yards wide (fig. 11). These are usually bordered by a narrow shrub zone between the sand ridge and the meadow, including *Alnus incana*, *Pyrus arbutifolia*, *Rosa carolina*, and *Cornus stolonifera*.

FIG. 5.—*Chamaedaphne* meadow with *Picea Mariana* and *Larix laricina*

With the grasses and sedges in the smaller meadows are found also *Hypericum virginicum* and *Spiraea salicifolia*, while occasional specimens of aquatics occur, as *Iris* and *Sagittaria*. In one case a remarkable growth of *Lobelia cardinalis* covered one acre of meadow with its scarlet flowers.

The bogs are generally found at or near the border of a lake or river, and are of two general types, one an ericad heath, the other a tamarack thicket. The heath type has a more or less continuous cover of sphagnum with its usual accompaniments: *Sarracenia purpurea*, *Vaccinium macrocarpon*, *Drosera rotundifolia*, *Menyanthes*

trifoliata, *Aspidium Thelypteris*, and in the wetter portions *Typha latifolia*, *Iris versicolor*, and *Phragmites communis* (fig. 5). The shrubs are *Chamaedaphne calyculata*, *Andromeda glaucophylla*, *Vaccinium corymbosum*, *Betula pumila*, and rarely *Ledum groenlandicum*. The trees if any are scattered, and include *Larix laricina*, *Picea mariana*, and where the substratum is very dry *Pinus resinosa* and *P. Strobus*.

The bogs of the thicket type are covered with a dense growth of *Larix* with some *Thuja occidentalis*, mingled with shrubs of *Alnus*

FIG. 6.—Long Lake, with pines on sandy point; Algonquin shore line in distance

incana, *Betula pumila*, *Rosa carolina*, *Chamaedaphne calyculata*, *Andromeda glaucophylla*, *Cornus stolonifera*, *Eupatorium perfoliatum*, *Myrica Gale*, and occasional specimens of *Cypripedium* sp. These thickets are usually surrounded by a zone of *Thuja*, sometimes narrow but occasionally of sufficient area and maturity of trees to be called a "cedar swamp." Here are found in addition *Fraxinus americana*, *Betula alba*, *Abies balsamea*, and *Acer rubrum*. Around the outer edges next the sand ridge, small specimens of *Tsuga canadensis* are locally found.

In the cedar forests the shade is very heavy. The roots of the trees interlace above the water or semiliquid muck, while the under-

growth grows on the peaty soil which has collected in hummocks or on the layer of tree roots. Shade-tolerant mosses are abundant, and occasional restricted patches of sphagnum occur. Among flowering plants the most common are *Coptis trifolia*, *Cornus canadensis*, *Trientalis americana*, *Maianthemum canadense*, *Aralia nudicaulis*, *Gaultheria procumbens*, *Viola* spp., and occasionally *Clintonia borealis*. *Aspidium spinulosum* and *Osmunda regalis* are frequently found, and some *Taxus canadensis*.

FIG. 7.—Algonquin shore, kept steep by erosion of Otter Creek

VEGETATION OF RIVER AND LAKE BORDERS.—In the Platte Plains there are no true alluvial floodplains, and the shores of streams and bodies of water are either rather steep sandy slopes, or else shallow bays or lagoons inhabited by one of the types of communities already described (figs. 6, 12). The lakes are frequently shallow some distance from shore, and these shallows generally contain extensive colonies of *Scirpus*. There is usually a fringe of aquatic plants, including *Typha latifolia*, *Sparganium*, *Sagittaria*, *Scirpus*, etc., or of shrubs including *Myrica Gale* and *Decodon verticillatus*. On flowing streams the latter does not seem to advance from year to year, probably on account of being torn away by ice in the spring. In

this region *Decodon* is chiefly confined to streams, as it has been observed on lakes or ponds in only one or two instances.

VEGETATION OF MORAINIC UPLANDS.—The morainic uplands were covered with a typical climax beech-maple-hemlock forest, which has been sufficiently described elsewhere (**10, 12**). In some places this is almost untouched, and in at least two places, near Lake Michigan on the west and south of Long and Rush Lakes, the tension zone between it and the sand ridge vegetation is in practically its original condition. In the first locality this zone is about a quarter of a mile wide, and its elements mingle with those of the sand ridge formation. On the south it descends the steep Algonquin terrace to the shores of Long Lake, and merges with the cedar forest between Long and Rush Lakes, and south and east of Platte and Little Platte Lakes (fig. 7). North of Little Platte it originally stopped on the crest of the steep bluff which borders the Otter Creek valley, and the bluff was occupied by a xerophytic conifer association, of which only a few patches now remain.

Development of communities

As already stated, the purpose of genetic synecology is to indicate the successional relationships of the communities of a region, and the place of each in a developmental series. In the present study there is no rock substratum present, and only a very restricted amount of clay or gravel, so that the communities found are largely confined to the psammosere and the hydrosere. Secondary successions are present, both in burned areas and to a limited degree in clearings, but in the present paper the chief concern will be to trace the stages of the original succession (prisere). With one or two minor exceptions the influence of climatic and physiographic factors is so slight as to be negligible, and the region is so young geologically that there seems to be no necessity for the consideration of paleoecological relationships.

SAND SUCCESSION (PSAMMOSERE)

PIONEER STAGES.—*Xerarch.*—The pioneer stages of this succession are confined to the strip of shifting sand along the lake. The initial vegetation includes *Ammophila arenaria* as the absolute

pioneer, associated with *Artemisia caudata*, *Calamovilfa longifolia*, *Cirsium Pitcheri*, *Campanula rotundifolia*, *Cakile maritima*, *Lathyrus maritima*, *Prunus pumila*, *Salix longifolia*, *S. syrticola*, *Senecio vulgaris*, *Solidago* spp., *Aster* sp., *Zygadenus chlorantha*, *Hudsonia tomentosa*, *Arctostaphylos uva-ursi*, *Juniperus communis*, and *J. horizontalis*. All of these are able to germinate on dune sand, but only *Ammophila* is able to become established in pure sand. The others are stunted and soon die, unless their roots come in contact with buried plant material, from which apparently they are able to obtain the necessary mineral elements. *Ammophila* and perhaps *Calamovilfa* are the only plants which cover the ground thickly enough to act as stabilizers. The other herbaceous plants are also scattered, and never grow close enough to form a ground cover in the moving dune belt. *Arctostaphylos* and *Juniperus horizontalis* germinate occasionally on the open sand, but it is doubtful whether they can stabilize. Whenever they occur in sufficient quantity to cover the ground, it is usually by invasion from a patch already established.

Hydrarch.—*Juncus balticus* and willows are the usual pioneers in pannes. Occasionally a local patch of *Pinus Banksiana*, with more or less *Thuja occidentalis*, *Abies balsamea*, and *Betula alba*, forms a clump or grove, which may reach the size of several acres and spread over small valleys or local patches of level sand. There is no evidence of any extensive permanent stabilization by coniferous trees in the belt of moving sand next to the lake. They frequently occur as narrow strips or tongues between advancing lee slopes. The transition from this area to the pine-oak ridges is very marked as one crosses the irregular line of crescent-shaped lee slopes and comes to the lower rounded ridges, where the force of the wind is much less marked and the plants of the pine-oak stage have become established. From this it would appear that the coniferous tree stage originates in pannes, but does not really become widespread so as to form a forest into which the more mesophytic pines and oaks gradually migrate and become dominant, but that the coniferous patches are relatively scattered, and their only influence is as humus formers and as centers of distribution for certain elements of the pine-oak stage. Stabilization, therefore, is due to a diminu-

tion of the force of the wind, either on account of the increasing distance from the shore as the lake waters recede, or by the building up by the wind of high dunes which form a windbreak and protect the sand ridges.

PINE-OAK STAGE.—With the relative cessation of sand movement, coupled with increase of humus, the pine-oak stages begin. As might be expected, the content of vegetation on the ridges shows a certain amount of progressive change, both in floristic content and in the density of growth and mesophytism, as we traverse the

FIG. 8.—Grove of old pine, oak, and hemlock, probably protected by proximity to Platte River.

region from the vicinity of the lake toward the south (that is, from younger to older ridges). On the first ridges there is a preponderance of conifers and many relics of the herbaceous pioneers, especially *Artemisia*, *Smilacina stellata*, *Arctostaphylos*, and *Juniperus* spp. The first tree of this stage to come into the coniferous association of the open dunes is *Pinus Strobus*, followed shortly by *P. resinosa*. *Quercus ellipsoidalis*, *Q. alba*, and possibly *Q. velutina* follow rather slowly, and now may be found fairly evenly distributed in the more advanced portions of the area. *Acer rubrum* is very frequently met near Platte River, or in other somewhat moist

localities. *Betula alba*, *Populus grandidentata*, and *P. tremuloides* are fairly common all through the region. As has been stated, the region has been burned probably more than once, although fortunately not in recent years. The extent of area covered by any one burning is uncertain. Certain local differences in distribution can best be explained on the assumption that the burnings have not been very complete; certainly some patches which bear old pines and hemlocks must have escaped (fig. 8), but patches of white birch and poplars indicate a secondary succession after fires.

FIG. 9.—Luxuriant growth of *Pteris aquilina* in mesophytic habitat, second growth birch and poplar in background.

The undergrowth varies from the modified pioneer type of the ridges nearest the lake to a mesophytic type containing many forms belonging to the climax beech-maple-hemlock forest. These mesophytic associations are not distributed in accordance with the geologic age of the ridges, but are determined rather by edaphic conditions. They will be considered in the section on the beech-maple-hemlock invasion. In addition to the typical mixed ground cover already described, there are two types of undergrowth societies unevenly distributed over the ridges, an almost pure *Pteris aquilina* society and a *Vaccinium* society including *V. penn-*

sylvanicum, *V. vacillans*, with considerable *Gaylussacia baccata*. On the whole, the *Pteris* communities are more characteristic of the portion of the ridge area west of the Platte River and the *Vaccinium* of that east of the river. No definite factors determining the distribution of these communities have yet been established. The *Pteris* seems to be more moisture-requiring than the *Vaccinium*, and it certainly grows more luxuriantly in the moister habitats (fig. 9). The *Vaccinium* species are usually regarded as more acid-tolerant, and investigations along these lines may yield definite results.

BEECH-MAPLE-HEMLOCK STAGE.—It is generally recognized throughout Michigan that the deciduous hardwood forest is confined to rich clay or loamy soil, white pine forests are found on sandy loam, and the pioneer conifers on poor sandy soil. The development of a climax deciduous forest on fixed dunes, as found in the Point Betsie region and at other points along the Michigan shore, is an interesting problem, the solution of which should materially be aided by the evidence to be obtained from a study of this relatively untouched region. As suggested by the preceding morphological study, the climax forest which developed on the morainic upland has begun to invade the sand ridge area along all lines of contact between the moraines and the sand, the undergrowth having gone farthest, and the tree species migrating more slowly. The first tree of the climax forest to appear in the sand ridges is *Tsuga canadensis*, scattered specimens of which are found up to a quarter or half a mile from the morainic border in the tension zone on the west, and for varying distances on the other borders of the sand ridge area. Many parts of the lowland border on the south have been cleared of trees, but in the small triangle between Long and Rush Lakes the deciduous forest is in contact with a cedar swamp, and we can find there a horizontal succession in practically untouched condition. The first hardwood pioneers in the swamp are *Fraxinus americana*, *F. nigra*, *Ulmus americana*, *Tilia americana*, and *Acer rubrum*. As *Thuja* disappears, the trees of the beech-maple-hemlock forest begin to come in on an alluvial substratum, forming a lake plain washed down from the Algonquin

terrace on the south. The largest trees have been cut, but hemlock stumps up to four feet in diameter are still to be seen.

On the strip of land between Long and Platte Lakes a scattered and somewhat stunted growth of *Tsuga canadensis*, *Acer saccharum*, and *Fagus americana* extends north almost to Michigan Highway 22, over soil which at first is somewhat alluvial, but which gradually changes into the usual sand ridge type. Toward the north the hard maples disappear first and the hemlocks last, as the oaks and pines become more frequent. On the east very little uniform advancement of the deciduous trees was found, probably because of the steep xerophytic bluff occupied by conifers (fig. 7). The valley of Otter Creek has not been studied in detail as yet, but it seems to be largely occupied by conifers, although the soil conditions are more those of an alluvial floodplain than in any other part of the sand ridge region.

Apart from this rather uniform invasion along the borders, there are several isolated spots where hemlocks at least are found in some frequency and of considerable size. On the morainic ridge between Platte and Little Platte Lakes the deciduous forest was apparently well developed, with, however, a large proportion of pines and some oaks. Large hemlocks are found in several places along the east bank of Platte River north of Platte Lake (fig. 8), and in the valley on the south slope of the morainic fragment on the shore of Lake Michigan (fig. 10). In the last locality they are in poor condition, and some have recently died. Small specimens are to be found on the edges of many of the smaller swamp depressions, especially on the southwest of Loon Lake, that is, on the opposite side of Platte River from the morainic ridge extension just mentioned. *Fagus americana* has not been found away from the borders and the wedge-shaped invasion between Platte and Little Platte Lakes. A solitary specimen apparently about fifty years of age is growing by Michigan Highway 22, about a quarter of a mile west of Platte River, and therefore in the heart of the sand ridge area. Its shape shows that it grew in the open, but its age does not preclude the possibility of its having been planted by the first settlers. The mixed coniferous-deciduous lake bluff border association described

in the Crystal Lake Bar region (10) does not appear in this region, probably because the corresponding habitat is not present. This association contained *Thuja occidentalis*, *Abies balsamea*, *Tilia americana*, and *Ostrya virginiana*, mixed with the trees of the climax deciduous forest on the crest of the bluffs facing Lake Michigan. It was apparently due to the exposure to sun and lake winds, combined with low soil moisture content. The only place where it might have been expected was on the high bank at the eastern edge of the

FIG. 10.—Morainic remnant on shore of Lake Michigan; landward slope equally steep, with hemlocks growing in valley.

sand ridge region, and there the only conifers seem to have been *Pinus Strobus* and *P. resinosa*.

The preceding discussion indicates that the migration of the beech-maple-hemlock forest into the sand ridge formation has been of two sorts, one a general advance along all lines of contact between the two formations, the other in a long slender belt on the morainic ridge and its remains, to the shore of Lake Michigan (fig. 10). Unpublished investigations by the writer indicate that for the establishment of *Thuja occidentalis* and *Abies balsamea* on sandy soil it is necessary that there should be present in the sand enough moisture to carry the young tree root below the drought zone. This

may be held by humus in the soil, or by a high moisture content in sand relatively free from humus, and it seeems possible that this may also be true for *Tsuga*, but not for *Fagus*. *Acer saccharum* seemed to hold an intermediate position between the two, and its apparent absence from any advanced positions on the sand ridge habitat was a distinct surprise. Morainic soil equally with humus seems to afford a suitable substratum for the establishment of all the species mentioned, either because of the supply of necessary mineral elements, or because these minerals make possible a better utilization of the water present. For these reasons the advancement of the deciduous formation seems to be the result of increased humus content and mesophytism, and also a pushing forward by sheer force of numbers. The parent seed trees being so near at hand and supplying so many seeds, it follows that in time a fair number of seedlings have been able to find conditions favorable to growth and so become established. In the other case, the morainic substratum affords a soil peculiarly favorable to the deciduous trees, and while a much smaller number of seeds have lodged on it, a relatively larger proportion have become established. In view of the fact that the shade and moisture conditions vary greatly on different parts of this ridge, it would seem to be the chemical constituents of the soil which give to it its favorable characteristics.

The question may be raised as to whether this condition may not be the result of the prehistoric fires, previous to which the beech-maple-hemlock elements may have been more widely distributed, and the present isolated groups may be relics preserved because of the protection of bodies of water. Against this view may be set the evidence of tradition and the entire absence of stumps in other moist habitats of the region which seem to have been untouched by fires. Unquestionably even hemlock stumps and logs do not last as long as pine, but it might be expected that some traces would remain if they had been at all widespread in comparatively recent times. This, however, would not account for the appearance of hemlocks on the edges of swamps at some distance from these relic patches. It is also reasonable to suppose that reforestation after a fire would proceed along general lines similar to those of

the original advance, so that in either event the stages of the prisere would be approximately as outlined.

Aquatic succession (hydrosere)

The substratum in this succession is standing water, either in closed depressions such as ponds and small lakes, or in open depressions as bays or lagoons along the banks of lakes or of Platte River. These various bodies of water show practically the same vegetation for the first three stages, commonly designated as the *Potamogeton*, *Nymphaea*, and *Scirpus* stages. After that different lines of succession are found, depending on the condition of the habitat.

Sand ridge depressions containing standing water.—In these depressions the water is fairly shallow, but the depression is surrounded by sand ridges whose slopes rise directly from the water's edge. Here are to be found either swamp or bog stages according to the condition of the substratum. In the swamp type the fourth stage is a narrow sedge zone, the shrub growth is scanty, mostly willows, and the sand ridge vegetation descends the slopes almost to the water's edge. In the bog type the quaking mat is seldom found, but there is a dense growth of sedges and grasses on a fairly solid muck foundation. This contains such bog plants as *Menyanthes trifoliata*, *Potentilla palustris*, and occasionally *Sarracenia purpurea*, and *Sphagnum* sp. The shrub zone is a dense thicket of *Alnus incana*, *Pyrus arbutifolia*, with some *Hamamelis virginiana*, and sometimes with scattered specimens of *Thuja occidentalis* and even *Tsuga canadensis* mingling with poplars and the first trees of the pine-oak association. The water is frequently shallow on the north side of the pond, possibly from sand blown in by the winds from Lake Michigan, and of course is exposed to the heat of the sun, but protected from the colder winds. The south side has deeper water, and is more sheltered from the heat of the sun on account of the shade of the pines and oaks, but exposed to the cold winds. In depressions of this kind the swamp vegetation is found on the shallow, warmer, northern side, while the bog type occurs on the deeper, cooler, southern side. In depressions which are sheltered on all sides and in which the water is deep all over, the bog type generally prevails over the whole pond.

GRASS MEADOW TYPE.—Here the fourth stage is one dominated by grasses and sedges forming a relatively solid turf. In the smallest depressions the sedge society may be only a few yards square, and in it there are often found swamp plants such as *Hypericum virginicum*, *Spiraea salicifolia*, and *Rosa carolina*, as well as occasional relics of the aquatic stages. The later stages resemble those of the swamp type already described. The larger grass meadows are relatively limited in number, only four or five having been discovered so far, and they have certain peculiar features which seem to demand special consideration. The first is the mature condition of the extensive grass turf, and the other is the absence of any tendency of the shrubs and trees to invade the meadow. Where the grass meadow is surrounded by a shrub zone of the swamp type, this may be accounted for on the assumption that the depression was originally all very shallow, thus favoring a development of turf so rapid that the shrubs and trees had no chance to become established before the mat of grass roots had completely occupied the substratum. There are, however, some features which indicate that the grass mat was formed recently and very rapidly, indicating perhaps a physiographic change in comparatively recent times. These are best shown in a grass meadow visited only once, as it was discovered in a hurried reconnoissance trip, and so far there has been no opportunity for a second visit. This meadow is located just west of the lower reaches of the Platte River very near the strip of moving dunes on the shore. It extends from northeast to southwest practically in a straight line for rather more than half a mile, but is less than a hundred yards wide at the point crossed, although somewhat wider to the east and the west. At this point there were imbedded in the grass on both edges of the meadow trunks of dead trees extending out from both banks, and on each tree was growing a row of tamaracks apparently not over twenty-five years old. There were scattered tamarack trees on the lower edges of the sand ridges. While the localization of the tamaracks on the dead logs and not in the grass is not surprising, the preservation of the logs long enough for the grass turf to form and the apparent youth of the trees makes a very interesting problem. This meadow apparently has never been mowed or burned. The

logs may have come from trees killed by prehistoric fires, as they had no bark on them, but they were not charred, and otherwise seemed well preserved, with many dead branches extending up among the young tamarack trees. In fact, the whole situation suggested the sudden freezing of the surface of a pond, solidifying into a green grass mat, instead of a covering of ice. In the case of the large meadow occupying a shallow swale between Long and Rush Lakes, which at one time might have been a water connection between the two lakes, the shore showed the regular horizontal

FIG. 11.—Grass meadow near Long Lake; bog shrubs on left, with tamaracks and cedar swamp behind them.

stages of a bog-cedar forest succession, but the center of the swale is occupied by a meadow with solid turf (fig. 11). The meadow has been mowed for years, and was recently ditched for draining, but this treatment apparently has not changed the general relations. The shrub zone at its southern edge is the usual bog shrub stage, followed by a belt of tamaracks of considerable size. A mature cedar forest adjoins this on the south, with a fairly dry substratum and some of the undergrowth elements of the deciduous forest. Next come deciduous swamp trees, and finally the trees of the climax forest. Here we have a bog forest left high and relatively dry, with a grass meadow formed at its edge.

Each of these formations, although differently situated (one in the heart of the sand ridges, the other between two lakes), seems to indicate the same physiographic change, that is, a sudden lowering of the water table by several feet. This change might be referred to the activities of the first white settlers about fifty years ago. The Long Lake area is very close to Crystal Lake, and might have been partially drained by seepage when Crystal Lake level was lowered in 1871 (10). A low terrace on the south bank of Long Lake adds weight to this hypothesis. The other meadow must have come very close to Platte River at its eastern extremity, and may have been lowered in connection with the first lumbering operations at about the same time.

Another explanation of the lowering of the water is based on diastrophic changes. Observations on the shore of Lake Michigan, both on the Michigan side and on the Green Bay Peninsula opposite, indicate that fifty years ago the lake was several feet higher than the highest levels of recent years, and this fall of level might have affected the level of Platte River in its lower reaches (fig. 12). There are also extensive meadows bordering Platte River and the sluggish stream connecting Platte and Little Platte Lakes, whose origin may be connected with the lowering of water levels at about the same time. Further study, both of the floristic content and of the nature of the substratum, is necessary before definite conclusions can be reached. There is no indication of any migration of trees into a grass meadow with solid grass mat, whether large or small, but there seems to be some evidence that they can come in on a floating mat of the swamp type. Further investigation may show that the latter case is really a bog mat, in which event it would not be available as evidence, and the presence of trees would be quite in accordance with the rule for bog mats.

Bog type.—Here the fourth stage develops as a bog mat composed of sphagnum and the usual accompanying bog plants. In several cases this has developed into an ericad heath composed largely of *Chamaedaphne*, *Andromeda*, occasionally *Ledum* and similar shrubs, including *Betula pumila*, and scattered trees of *Larix*, *Picea mariana*, and occasionally *Pinus Strobus* and *P. resinosa*. In other cases the tamaracks with some bog shrubs and

Thuja have come in very thickly, forming a bog thicket which in some cases apparently may develop into a cedar forest. The tamaracks in this region are all small, with the exception of those between the shrub belt and the cedar forest already noted between Long and Platte Lakes. The occurrence of bog vegetation in the depressions among sand ridges has already been noted. The variation in depth on opposite sides also applies to some extent to the larger ponds and lakes. In the latter cases the shallow portions are characterized by extensive *Scirpus* colonies, but the bog asso-

FIG. 12.—Lower reaches of Platte River, bordered by grass meadows, with some second growth birches; sand ridges in distance.

ciations do not appear along the shores of the lakes. In open bays and lagoons there was no general uniformity, but swamp or bog types were found corresponding to the varying local conditions. From this it is concluded that the development of the later stages of the hydrosere into the swamp or the bog type is dependent chiefly on depth of water and temperature. Investigations as to acidity have not been made as yet, but it is assumed that here, as elsewhere, the swamp type will be associated with a neutral or alkaline condition and the bog type with high acidity. The tree stage in the hydrosere was found to follow only the quaking mat

stage, and not the grass meadow. If we accept the hypothesis for the very recent formation of the large grass meadows, the absence of trees might be attributed to shortness of time, but the same condition is found in the smallest meadows, which from their position and general appearance must be regarded as contemporaneous with the wet depressions and with the sand ridges themselves, and here there should have been ample time for invasion. It does not follow necessarily that the grass meadow is an edaphic climax, but it is evident that that association will remain stable for a very long time. As already noted, the bog mat passes relatively rapidly into a tamarack cedar forest, which quickly receives hydrophytic deciduous elements, and thus passes into the climax deciduous forest.

Summary

1. Genetic synecology is that part of ecology which deals with the developmental relations of plant communities. In a limited region the development of successions (seres) is definitely related to the character of the substratum. In this region two such seres are found, the sand succession (psammosere) and the aquatic succession (hydrosere). The clay-gravel succession (geosere) has reached its climax on the surrounding moraines, and is observed only as it invades the sand ridge region.

2. In this study the successional units, the concrete association and formation, are defined as follows. The association is a plant community of essentially uniform (or homogeneous) physiognomy and ecological structure, and of essentially uniform (or homogeneous) floristic composition as regards dominant species. The formation is an association-complex characterized by a dominant association, but including all adjacent associations, whether mature or immature, and other more or less anomalous or unidentified communities associated with them. The unit above the formation is a formation complex, or aggregate, and is composed of the formations of a definite region which may be limited by climatic or geographic boundaries. The ground occupied by an association is called a locality, that occupied by a formation an area, and that occupied by a formation complex a region.

3. The vegetation of the region studied is found to be a formation complex consisting of a sand dune formation, a sand ridge

formation, and swamp and bog formations. It occupies a region which consists of sand ridges with depressions containing bodies of water of all sizes, from a few yards to a mile or more in diameter. Geologically the region was a shallow bay of Lake Algonquin drained by the recession of the waters of the lake with the melting of the ice barrier in the Straits of Mackinaw.

4. The first stages of the sand succession (psammosere) are found in the moving dune belt along the shore, but they do not lead to a complete stabilization of the sand. The later stages appear when the sand stops moving as a result of a checking of the force of the wind, due to distance from the shore or the formation of high dunes which act as windbreaks. The pine-oak stage shows a progressive change from the less mature areas near the lake to the more mesophytic areas in the southern portion of the region. Soil moisture content and the amount of humus in the sand seem to be important factors in this change.

5. The clay-gravel succession (geosere) has reached the climax stage as a beech-maple-hemlock forest on the surrounding morainic upland, and is found invading the pine-oak formation along the borders of the region, and especially along a narrow morainic tongue which extends completely through the sand ridge substratum to Lake Michigan. The controlling factor in this invasion seems to be primarily the chemical character of the soil, glacial material ranking close to humus in importance, and secondarily the soil moisture content.

6. The various ponds and lakes all show the normal early stages of the aquatic succession (hydrosere), which lead either to swamp meadows or to bog forests, the line of development followed being determined chiefly by depth of water and exposure to the heat of the sun.

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SULPHUR CONTENT OF SOILS AND ITS RELATION TO PLANT NUTRITION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **297**

SCOTT V. EATON

(WITH ONE FIGURE)

Introduction

Ever since the ten essential elements for plant nutrition were established by the work of SACHS, BOUSSINGAULT, NOBBE, and other investigators, sulphur has been recognized as one of them. The ash analysis method of determining sulphur in plants, however, which was in use during this early period, showed such a small amount present that the needs of the plant were thought to be amply taken care of by the supply in the soil. Contributions during the last twenty years by BERTHELOT, BARLOW, FRAPS, GOSS, BESTLE, SHERMAN, and others have shown that in ashing plant material much of the sulphur may be lost. The amount of sulphur in plants as determined by analyzing the ash may be only a fraction of the real amount. Thus the whole question of the relation of sulphur to plant nutrition has been reopened, for if plants use several times as much sulphur as had been supposed, then perhaps the supply in the soil is not sufficient for the needs of the plant. Recently there have been a number of contributions to the subject. The first questions to be considered have naturally been how much sulphur do crops use and what are the supplies to meet these needs. Thus the first problems to be investigated have been the sulphur content of crops, the sulphur content of soils, the amount of sulphur brought down by the rain, and the amount lost by drainage, etc. Next, sulphur was added to soils found to be low in it to see whether the yield of crops would be increased. In the present paper no attempt is made even to approximate a resumé of the sulphur literature, rather complete digests of which may be found in papers by CROCKER (**4**) and OLSON (**19**).

ROBINSON and co-workers (**22, 23**) have analyzed a number of soils from different parts of the United States. The sulphur content is not high, the average for thirty-five important agricultural soils being 0.052 per cent, with a range of 0.012–0.156 per cent. SHEDD (**24**) finds the soils of Kentucky much poorer in sulphur than in phosphorus, and is inclined to place sulphur in the same class with phosphorus, potassium, and nitrogen as one of the chief limiting factors in crop production. In pot experiments with some of these soils, tobacco, soy beans, turnips, radishes, mustard, and alfalfa were benefited by sulphur fertilization. AMES and BOLTZ (**1**) report analyses for certain Ohio soils. The unfertilized soils range in sulphur content from 0.020 to as high as 0.055 per cent. BROWN and KELLOGG (**2**) find nearly twice as much sulphur as phosphorus in some of the larger soil areas of Iowa. The Mississippi loess proves to be lowest, the soil samples in this area ranging in sulphur content from 441 to 847 pounds per two million pounds of soil. SWANSON and MILLER (**27**) have analyzed a number of the soils of Kansas and find that the cultivated soils analyzed have an average sulphur content of 0.027 per cent. Certain cultivated soils of Wisconsin, analyzed by HART and PETERSON (**8**), prove to be low in sulphur, the average being 0.020 per cent. They summarize the results of their analyses of a number of crops by stating that cereal crops remove from the soil about two-thirds as much sulphur trioxide as phosphorus pentoxide, the grasses of mixed hay as much sulphur as phosphorus, while the legume hays may take from the soil about as much sulphur as phosphorus, or, as in the case of alfalfa, more sulphur than phosphorus. Such crops as the cabbage and the turnip may remove two to three times as much sulphur trioxide as phosphorus pentoxide. REIMER and TARTAR (**21**) give analyses for a number of Oregon soils. The range in the sulphur content of the surface soils is 0.015–0.038 per cent. The phosphorus content is much greater. The sulphur fertilization of alfalfa grown on these soils produces greatly increased yields. Increased tonnage yields of 50–1000 per cent are secured, and the protein content is increased in some cases almost 2 per cent. In experiments in Washington by

OLSON (19), sulphur fertilization of alfalfa caused increased yields of 200–300 per cent.

The purpose of the present investigation was (1) to increase our knowledge of the sulphur content of soils, and (2) to study the relation of sulphur to chlorophyll development in certain plants and its effect on the yield of these plants. The phosphorus content of all the soils was also determined. Phosphorus, together with nitrogen, is considered the most generally limiting element of crop production in the soils of the United States. It was thought that it would be interesting to compare the sulphur content of the soils with their content of such an element as phosphorus.

Investigation

SOIL ANALYSIS

It is important for American agriculture to discover how many soils in the United States are suffering from lack of sulphur, as are the Oregon soils to which reference has already been made. The Oregon results might be duplicated, perhaps, in the case of many other soils; on the other hand, many soils are probably not lacking in sulphur. The samples were chosen with a view of giving some idea of what range in sulphur content might be expected in the soils of the eastern and central United States. Thus, samples from the Atlantic and Gulf coast regions, from one of the southern states, from certain of the north central states, and from Chicago were analyzed. Investigations on the Atlantic coast during the early history of the United States showed great benefits from the use of gypsum as a fertilizer. It was thought that the analysis of certain of the coast soils might give some interesting results. On the other hand, soil analyses and sulphur fertilization tests in the central states may be said to indicate, in general, a higher sulphur content in the soils of this section than in the coast soils. It was desired to analyze a number of soils of the central states to compare with the coast soils. It is well known that rain carries down much more sulphur from a smoky atmosphere than from one less contaminated with smoke. It was thought that the Chicago soils might prove to have a very high sulphur content, owing to this fact.

Methods

Three methods of total sulphur determination were tested, the sodium peroxide method as evolved by HART and PETERSON (8), the VAN BEMMELEN method as modified by the same investigators, and a sodium carbonate fusion method, which was really a combination of KOCH'S (12) sodium carbonate method for the determination of total sulphur in organic material and HILLEBRAND'S (10) sodium carbonate method for the determination of total sulphur in rocks. The sodium peroxide method gave as high results as the other methods and better duplicates, and also was easier to manipulate. It was therefore adopted, but modified somewhat, and so it is given in some detail.

Ten grams of soil was placed in a 100 cc. nickel crucible, made quite moist with water, and 10 gm. of sodium peroxide added, a little at a time, stirring thoroughly with a nickel rod as the sodium peroxide was being added. This was heated slowly with a microburner until dry, and 10 gm. more of sodium peroxide added, spreading it over the surface, and continuing the heating until the surface layer melted. With a blast burner the mass was then brought to red heat and kept in this condition for ten minutes, stirring thoroughly. This was allowed to stand over a moderate flame for one hour, cooled, and the fused mass removed with boiling water, transferring it to a 600 cc. beaker. This was neutralized with concentrated HCl and then 10 cc. excess added, and allowed to stand on the steam bath for five or six hours, or until there was no undecomposed material in the bottom. It was next transferred to a 500 cc. volumetric flask, cooled, filled to the mark, and allowed to stand for four or five hours, shaking at intervals. A 250 cc. aliquot was filtered off, transferred to a beaker, a quantity of filter paper pulp added, and while stirring the iron, aluminum, etc., was precipitated out with ammonium hydroxide. This was heated for an hour on the steam bath, filtered into an 800 cc. beaker, and the precipitate washed with hot water until 600 cc. was obtained. After this it was heated to boiling, 10 cc. of hot 10 per cent barium chloride added to the boiling solution, and allowed to stand on the steam bath over night and at room temperature for the remainder of the twenty-

four hours. The volume must not be allowed to decrease while on the steam bath. The solution was then filtered off from the barium sulphate, washed until no test for chlorides was obtained, the precipitate dried in an oven, and ignited to constant weight in a muffle furnace.

Part of the sulphur determinations reported later in this paper were obtained by igniting over a microburner, taking care that the paper was consumed without flaming up, but it was found that more uniformly successful results were obtained by igniting in a muffle furnace.

The iron and aluminum were removed because it was found that, in the case of a number of the soils analyzed, the barium sulphate precipitate was quite seriously contaminated by the iron. In the case of some of the soils analyzed during the preliminary work, the iron collected in masses on the bottom of the beaker. In other cases there was no contamination, or so little that the error introduced was small. It was decided, however, to make it a general practice to remove the iron and aluminum before adding the barium chloride solution. The chief difficulty encountered in the process was in washing out the sulphate ion from the iron and aluminum hydroxides. By using hot water, however, and having the precipitate well separated with paper pulp, the sulphate ion was completely washed out. It was found that there was some sulphur in the reagents used. Blanks were run and correction made for this.

The phosphorus was determined by the magnesium nitrate method as given in the Methods of Analysis of the Association of Official Agricultural Chemists (17). No important modification was made in the method. The ignition value given is the loss in weight obtained by heating the soil in the muffle furnace at red heat for an hour and a half. Two or three grams were used, and it was found that after heating for this length of time there was no loss of weight on further heating.

Data

In the following results of the analyses, the samples that proved to have the lowest sulphur content will be given first. The chief

lack in the data is information as to the previous history of the soils from which the samples were taken. In a number of instances I have data as to the productivity of the soils, and information as to the amount of manure and fertilizer that had been applied to the soils in recent years, but in some cases it was impossible to secure this information. Also, the data would have more general significance, perhaps, if in all cases the names of the soil types could

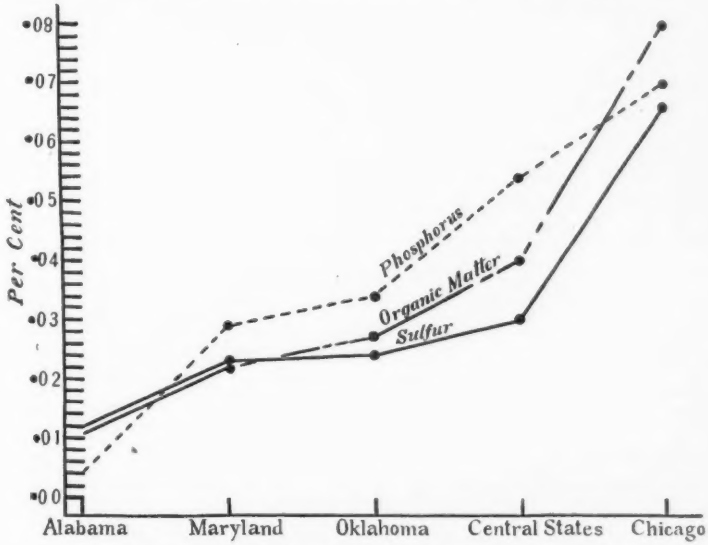

FIG. 1.—Curve comparing sulphur, phosphorus, and organic matter content of five groups of soils; organic matter divided by 200.

be given, but this was only possible for the Maryland soils. In most instances, however, the samples were taken from important agricultural soils, and therefore the data should have significance in adding to the information as to the sulphur content of the agricultural soils of different sections of the United States. All the results are figured on the basis of the oven-dry weight. The data concerning the pounds of sulphur per acre were obtained from the percentage of sulphur determined by analysis, by assuming that an acre of soil 6.5–7 inches in depth weighs 2,000,000 pounds.

Tables I and II give the results of the analysis of some soil samples from the Gulf coast and the Atlantic coast. I am indebted to Dr. A. G. McCall, of the University of Maryland, for the Maryland samples, and also for the information in regard to the productivity of the soils. Little information was obtainable in regard to the samples of table I, except that they came from soils

TABLE I

SULPHUR, PHOSPHORUS, AND ORGANIC MATTER CONTENT OF CERTAIN ALABAMA SOILS (NEAR MOBILE BAY), TAKEN FROM SURFACE

Sample no.	Percentage sulphur	Lb. per acre	Percentage phosphorus	Lb. per acre	Ignition value
15	0.0090	180	0.0028	56	2.189
16	0.0148	296	0.0044	88	2.127
17	0.0151	302	0.0067	134	2.256
18	0.0126	252	0.0044	88	2.204
Average	0.0128	256	0.0045	90	2.194

TABLE II

SULPHUR, PHOSPHORUS, AND ORGANIC MATTER CONTENT OF CERTAIN MARYLAND SOILS

Sample no.	Location (county)	Depth inches	Percentage sulphur	Lb. per acre	Percentage phosphorus	Lb. per acre	Ignition value
23	Worcester	0–7	0.028	560	0.015	300	2.48
24	Worcester	7–28	0.023	460	.....	.....	1.58
25	Talbot	0–7	0.023	460	0.026	520	4.39
26	Talbot	7–28	0.015	300	0.012	240	4.71
27	St. Mary's	0–7	0.018	360	0.026	520	4.66
28	St. Mary's	7–28	0.020	400	0.018	360	4.54
29	Howard	0–7	0.019	380	0.048	960	6.33
30	Howard	7–28	0.014	280	0.044	880	6.14
31	Prince George	0–7	0.030	600	0.030	600	4.81
32	Prince George	7–28	0.019	380	0.026	520	4.91
Average surface soils			0.023	460	0.029	580	4.53
Average subsoils			0.018	360	0.025	500	4.37

on which the attempt was being made to grow pecans. The soils are so low in sulphur, phosphorus, and organic matter that it would seem impossible to grow any crop successfully on them without considerable fertilizing.

Samples 23 and 24 of table II belong to the soil type known as Norfolk fine sandy loam. The field from which the samples were taken is fairly productive, being capable of producing ten bushels

of wheat or thirty bushels of corn per acre. The samples from Talbot County belong to the Elkton silt loam type of soil. It is not very productive, and has to be fertilized rather heavily to produce very good crops. The soil represented by samples 27 and 28 is known as the Leonardtown silt loam type of soil. It has rather low productivity, producing about 500 pounds of tobacco or seven bushels of wheat per acre. The samples from Howard County belong to the Chester loam soil type, which is one of the best soils in the state, producing sixty-five bushels of corn or twenty bushels of wheat per acre. Samples 31 and 32 belong to the sassafras silt loam type. This is a fairly good soil, producing ten bushels of wheat or thirty-five bushels of corn per acre. The samples from St. Mary's County and from Howard County are from soils that had not been fertilized in recent years. The other soils have probably received recently little if any fertilizers. The Maryland samples are rather few in number, but are well distributed over the state. They are probably typical for the cultivated soils of Maryland. The soils are low in sulphur, phosphorus, and organic matter; somewhat lower in sulphur on the average than in phosphorus. It would seem that they should be benefited by the use of both sulphur and phosphorus as fertilizers.

Table III is an attempt to make a further study of the Maryland soils, using as a basis the productivity data and the data for the surface soils of table II. The second column shows the relative order of the five soils in productivity, beginning with the most productive. There does not seem to be any relation between the sulphur content and the productivity. When we consider the phosphorus content, however, the two best soils as to productivity are also highest in phosphorus. This relation between phosphorus content and productivity does not hold in the case of the other three soils, but here the phosphorus content is so low that other factors may be limiting production. It would seem possible, therefore, especially in the case of the fields from which the Chester loam and sassafras silt loam samples came, that phosphorus rather than sulphur was limiting production. The Chester loam soil especially should be considered. It is one of the best soils of the state and in its phosphorus content also it is decidedly higher than

any other of the soils analyzed. The order of the soils as to the organic matter content is about the same as their order considered on the basis of the phosphorus content. It might be that the relatively large amount of organic matter in the Chester loam and the sassafras silt loam soils is a factor in their productivity. Organic matter improves the tilth of soils, adds plant food, and has other important effects.

Their relative ability to produce cereal crops is used as a measure of the productivity of the soils. Cereal crops require more phosphorus than sulphur. It might well be that, if the production of a high sulphur containing crop (alfalfa, for instance) was taken as the criterion, the order of the soils in table III would be different. Even if phosphorus, rather than sulphur, is at present the limiting

TABLE III

RELATIVE ORDER OF THE FIVE MARYLAND SOILS IN PRODUCTIVITY, SULPHUR, PHOSPHORUS, AND IGNITION VALUE

Soil type	Productivity	Sulphur	Phosphorus	Ignition value
Chester loam	1	4	1	1
Sassafras silt loam	2	1	2	2
Norfolk fine sandy loam	3	2	5	5
Leonardtown silt loam	4	5	3	3
Elkton silt loam	5	3	3	4

factor in these soils, sulphur would no doubt soon become the limiting factor if the level of supply of the phosphorus is raised by adding phosphorus fertilizers. The sulphur supply is so low that, with phosphorus removed as the limiting factor, it might become the limiting factor to production.

Of course it is realized that too great reliance should not be placed in a soil analysis, especially such a soil analysis as this, where only two of the several elements needed by plants are determined. At the most, a soil analysis only shows the total amount of plant food present and does not tell anything as to the availability of the elements. Also, other factors than plant food may be limiting production, but a soil analysis should develop some leads, which can be followed up by other methods of attack.

Since the data show a rather low sulphur content in the few Atlantic coast and Gulf coast soils analyzed, it might be of interest

to see what results have been obtained from using sulphur as a fertilizer in these regions. Very little work of this kind has been done. Several stations report a favorable effect from using phosphorus or potassium as a fertilizer for alfalfa, when the carrier of the phosphorus or potassium also contained sulphur. The Delaware station (**7**), for example, reports greatly increased yields of alfalfa due to acid phosphate. Experiments in Oregon (**21**) have shown a decided increase from applying acid phosphate to soils, but no increase due to phosphorus in any other form. Here it has been definitely proved that the increased yield caused by acid phosphate was due to the sulphur of the acid phosphate, and not to the phosphorus. It would seem worth while to test this in the case of the Delaware soils. The Virginia station (**3**) secures increased yields of alfalfa due to phosphorus in the form of acid phosphate and basic slag, but not in the case of other forms of phosphorus, such as rock phosphate. Here again we have the possibility that sulphur is responsible for the increased yields. The Massachusetts station (**16**) finds sulphate of potash a better fertilizer for alfalfa than muriate of potash. The alfalfa of the sulphate of potash plats was also a darker green. Clearly these results are due to the sulphur present in the sulphate of potash, and not to any differences in the potassium.

The best experiments on the Atlantic coast to show the effect of sulphur fertilization on crops are those of the investigators of the colonial period, whose work is summarized by CROCKER (**4**). PETERS and BINNS were the most prominent of these investigators. They performed numerous experiments showing the effect of gypsum on crop yield. Leguminous crops especially were benefited, red clover giving increased yields of two to threefold. BINNS reported like increased yields for corn and wheat. Although the reports of the experiments do not make this clear, it seems likely that the beneficial effects of gypsum on the non-leguminous crops was due to the increased nitrogen supply brought about by the greater growth of the legumes of the rotation. RUFFIN was also greatly impressed by the results obtained from the use of gypsum as a fertilizer. In his *Essay on calcareous manures* he speaks of the magic effects obtained from applying gypsum as a fertilizer to

clover. Considering the results of the writer's analyses, together with the other experimental work to which reference has been made, it would seem worth while to test sulphur as a fertilizer throughout the Atlantic coast region.

The samples of table IV were taken in cultivated fields near Miami, Oklahoma, two of the samples from one field and two from another. Nothing is known as to the previous treatment of the soils from which the samples came, or it might be possible to answer some questions which arise from a study of the data, such as the reason for the much greater phosphorus content of samples 21 and 22 than of samples 19 and 20.

TABLE IV

SULPHUR, PHOSPHORUS, AND ORGANIC MATTER CONTENT OF CERTAIN SOILS NEAR MIAMI, OKLAHOMA

Sample	Depth	Percentage sulphur	Lb. per acre	Percentage phosphorus	Lb. per acre	Ignition value
19.....	Surface	0.0202	404	0.0107	214	4.346
20*.....	Subsoil	0.0287	574	0.0087	174	7.764
21.....	Surface	0.0278	556	0.0587	1174	6.710
22*.....	Subsoil	0.0136	272	0.0543	1086	5.290
Average surface soil...		0.0240	480	0.0347	694	5.528
Average subsoils.....		0.0211	422	0.0315	630	6.527

* It is not certain that subsoils 20 and 22 go with soils 19 and 21 respectively; they were arranged with these soils on the basis of color.

Table V contains the results of the analyses of certain soils of the central states. Samples 3 and 4 were taken in an alfalfa field; samples 5 and 6 in an oat field. The alfalfa field had been manured with one and one-half tons of cow manure per acre in 1918. The oat field had received in the same year an application of two tons per acre of cow manure. Both fields had been fertilized with gypsum in 1920. Samples 7, 8, 9, and 10 were all taken in one field of seven acres, which had been in grass for many years. This field was put in corn in 1920, producing only a fair crop. In the fall of 1920 it was put in alfalfa. Sample 33 is a composite sample taken in a clover field near Paris, Illinois. Trouble was being experienced in growing clover on part of the field. It was thought that this might be due to the low sulphur content of this part of the field, but soil analysis indicated that such was not the

case. In fact, one of the samples from soil supporting a good stand of clover contained decidedly less sulphur than did any of the samples from the part of the field where there was no clover. It would seem that some other factor than the sulphur content was preventing the growth of clover. Since the results of analysis revealed no reason for the failure to secure a good stand of clover on part of the field, the data for all the samples were averaged in order to secure an average value for the entire field.

TABLE V

SULPHUR, PHOSPHORUS, AND ORGANIC MATTER CONTENT OF CERTAIN SOILS OF CENTRAL STATES

Sample no.	Location	Depth	Percentage sulphur	Lb. per acre	Percentage phosphorus	Lb. per acre	Ignition value
1....	Fremont, Ohio	0–7	0.029	580	0.056	1120	6.87
2....	Fremont, Ohio	7–20	0.015	300	0.048	960	6.72
3....	Plattesville, Wis.	0–7	0.028	560	0.034	680	4.47
4....	Plattesville, Wis.	7–20	0.038	760	0.040	800	5.62
5....	Plattesville, Wis.	0–7	0.034	680	0.040	800	5.26
6....	Plattesville, Wis.	7–20	0.019	380	0.036	720	6.74
7....	Naperville, Ill.	0–7	0.021	420	0.060	1200	10.17
8....	Naperville, Ill.	7–20	0.030	600	0.040	820	8.40
9....	Naperville, Ill.	0–7	0.040	800	0.051	1002	9.32
10....	Naperville, Ill.	7–20	0.020	400	0.052	1004	9.71
11....	Gilman, Ill.	0–7	0.058	1160	0.086	1720	13.53
12....	Gilman, Ill.	7–20	0.035	700	0.120	2400	10.76
13....	Gilman, Ill.	0–7	0.029	580	0.045	900	6.71
14....	Gilman, Ill.	7–20	0.036	720	0.057	1140	8.43
33....	Paris, Ill.	0–7	0.030	600	0.056	1120	7.40
Average surface soils			0.030	600	0.054	1080	8.00
Average subsoils			0.027	540	0.056	1120	8.05

Particular attention is called to the samples from Gilman, Illinois. These were received from Mr. F. I. MANN, who also supplied the information in regard to the previous treatment of the land from which the samples came. They were all taken in the same field. Samples 11 and 12 came from a part of the field that during sixteen years had received applications of rock phosphate and ground limestone. No other fertilizer had been applied to the land for at least twenty years, and not much before that. Samples 13 and 14 came from the check part of the field, which had received no fertilizer of any kind. Clover had been grown on the field once in four years, about half of the crop being plowed

under. Clover was also grown on the check part of the field. Very little grew here, however, and so there was not much to plow under. Mr. MANN stated that the amount of phosphorus applied to the land where samples 11 and 12 were taken would just about equal that naturally present in the soil, so that these samples would be expected to contain about twice the phosphorus of the samples from the check portion. Table V shows this to be the case, but the sulphur content of the surface soil of the fertilized land is also double that of the check portion. This is rather to be expected, when we compare the two in their organic matter content. Sample 11 is about double that of sample 13, and a high organic matter content usually means a high sulphur content. The question, however, is as to the source of supply of the sulphur. No sulphur fertilizers have been applied to the land. There is the possibility that, since the clover plant makes considerable growth during the time of the heavy rains of the spring and again in the fall after the rains start (times when the sulphur content of rainwater is rather high), some of the sulphur might come from this source. It is not believed, however, that the sulphur brought to the land by the rain results in a net increase in the sulphur content of the soil, on account of the large amount of sulphur lost in drainage, although the amount lost in drainage is greatly decreased when the land is covered by a crop. There is the additional possibility that the clover roots bring up sulphur from the subsoil, depositing it in the surface layers. As shown by the data, the subsoil of the fertilized part of the field has about the same sulphur content as the soil and subsoil of the check portion. Some of the other soil analyses have shown that the sulphur content of various parts of the same field may vary widely, when all parts of the field have been treated alike so far as sulphur fertilization is concerned. If this is true in the present case, then the difference in the sulphur content of the two parts of the field would not be significant, but the high organic matter content of the fertilized part of the field would seem to indicate that these samples are representative, and that there really is here a high sulphur content.

Considering all the samples of table V, it may be said in summary that the sulphur content on the average is not high in amount,

although somewhat greater than the Maryland and Oklahoma soils, and decidedly greater than the Alabama soils. The phosphorus content is also rather low, although much higher than the sulphur content. There is a fair amount of organic matter present on the average in the soils. Reference was made previously to certain soil analyses in Kentucky, Iowa, Kansas, Wisconsin, and Ohio. Judging from my analyses and those referred to in the introduction, many soils in the middle states need sulphur. Some of them are well supplied, however, and on the average they seem to have a higher sulphur content than the soils of either the Atlantic or Pacific coasts, although not enough analyses or fertility experiments have been made to make a positive statement as to this. On the other hand, some of the soils are as low in their sulphur content as any of the coast soils, so that it would not be surprising if sulphur should prove beneficial on these soils. Demonstration experiments on as many of the central states soils as possible are needed to determine how generally sulphur is deficient.

Not many experiments of this kind have been performed. Certain investigators in Kentucky (**25**), Wisconsin (**9, 28**), and other states, in pot experiments, have secured increased yields from sulphur fertilization in the case of alfalfa, clover, radishes, rape, turnips, mustard, tobacco, and soy beans. In field experiments, JARDINE and CALL (**11**) attribute the increased yields in Kansas secured by fertilizing alfalfa with acid phosphate to the phosphorus of the acid phosphate, but here again there is the possibility that the sulphur contained in the acid phosphate is at least partly responsible for the increased yields. During the last few years the Gypsum Industries Association has conducted a number of experiments, seeking to determine the value of gypsum as a fertilizer for crops. Beneficial effects have already been secured in a number of cases. Such work should be extended.

Table VI records the results of the analysis of a few samples taken within the environs of Chicago. Each sample includes a number of borings and is therefore composite. The sample from the South Chicago region was taken from what seemed to be a natural prairie. This soil had probably never been fertilized. The Midway, where samples 39 and 40 were taken, is quite often

manured. It was learned after analyses were made that samples 41 and 42 were taken from a part of the botany gardens that had been filled in. The subsoil especially of this sample is not typical, its higher sulphur content than the subsoils of the other soils probably being accounted for by the filling in. The few Chicago soils analyzed are all much better supplied with sulphur, phosphorus, and organic matter than any of the other soils analyzed. It may be that soils of as high a sulphur content as these Chicago soils might not need any sulphur fertilization, although in the case of certain high sulphur-using crops the available sulphur might not be sufficient. All the samples were taken from soils overlaid with sod, and have a high organic matter content. There

TABLE VI

SULPHUR, PHOSPHORUS, AND ORGANIC MATTER CONTENT OF CERTAIN CHICAGO SOILS

Sample no.	Location	Depth	Percentage sulphur	Lb. per acre	Percentage phosphorus	Lb. per acre	Ignition value
39....	Midway	0–8	0.060	1200	0.100	2000	15.25
40....	Midway	8–26	0.021	420	0.055	1110	10.24
41....	Botany Gardens	0–8	0.055	1110	0.073	1460	15.79
42....	Botany Gardens	8–26	0.045	900	0.068	1360	13.08
43....	South Chicago	0–8	0.069	1380	0.038	760	17.11
44....	South Chicago	8–26	0.023	460	.....	.....	15.12
Average surface soils.....			0.061	1220	0.070	1400	16.05
Average subsoils.....			0.029	580	0.060	1200	12.81

are probably many soils in Chicago of much lower sulphur and organic matter content, which might need sulphur fertilizers.

It was thought interesting to determine how much of the total sulphur of the Chicago soils might be accounted for by the sulphate sulphur content. As is well known, where much soft coal is burned, much sulphur is given off. It would be expected, therefore, that rain would carry to the soil much more sulphur from a smoky atmosphere than from one free from smoke. WARRINGTON (quoted by HART and PETERSON (**8**)) gives the amount of sulphur carried to an acre surface of soil at Rothamsted as about seven pounds per year. Judging from their limited data, HART and PETERSON (**8**) estimate about the same figures are correct for University Hill Farm, Madison, Wisconsin. Data indicate a much higher sulphur

content of the rainwater of cities. Some of my determinations show several times as much sulphur in Chicago rainwater as in rainwater collected in the country some distance from Chicago. Most of the sulphur in rainwater is in the sulphate form. It might be expected, therefore, that the sulphate sulphur present in the Chicago soils might account for much of the total sulphur. Roughly quantitative determinations showed an average sulphate sulphur content of the three surface soils of table VI of 158 pounds per two million pounds of soil. This is high, compared with the Iowa soils as analyzed by BROWN and KELLOGG (**2**). They found an average sulphate sulphur content of 59 pounds per two million pounds of soil, but the sulphate sulphur present in the Chicago soils accounts for comparatively little of the total sulphur. Most of this is in the organic form, and the high sulphur content of the soils is due mainly to the high organic matter content. That the sulphate sulphur content is not higher may be accounted for probably by the ease with which sulphur in a soluble form is leached from the soil.

LYON and BIZZELL (**14**), MACINTIRE and co-workers (**15**), and other investigators have performed lysimeter experiments. LYON and BIZZELL show that 3–6 times as much sulphur is lost in drainage as is used by the crop, and when put in a soluble sulphate added to the tanks, over one-half of the amount added in any one year was removed in drainage the same year.

Table VII summarizes the data of tables I, II, IV, V, and VI. Fig. 1 compares in a graphical way the sulphur, phosphorus, and organic matter content of the five groups of soil. The Alabama, Maryland, and Oklahoma soils are all low in sulphur, phosphorus, and organic matter, the Alabama soils being especially deficient in all three substances. The phosphorus, on the average, is not much greater in amount than the sulphur. Although the central states soils are better supplied with sulphur and phosphorus than these three groups of soils, they would not be considered high in either. The range in the amount of sulphur and phosphorus present in the various soils is rather great. Certain of the soils would be considered fairly well supplied with both sulphur and phosphorus. The organic matter content of the soils is on the

average fairly good, although here also the range is very great, and certain of the soils are deficient in this respect.

The sulphur and phosphorus content of the Chicago soils is fairly good, while the organic matter content is high. As is brought out in connection with table VI, the samples are not typical for the cultivated soils of Chicago and its environs. They were taken in places where the organic matter had had a chance to accumulate. Their high sulphur content is to be accounted for mainly by their high organic matter content, the sulphur brought down by the rain accounting for little of the total sulphur. Although the Chicago samples should not be considered typical for cultivated soils, they are perhaps typical of soils of any section of the United States which have been in grass or any form of plant

TABLE VII

SUMMARY OF TABLES I, II, IV, V, AND VI, GIVING AVERAGE OF SURFACE SOILS; SULPHUR AND PHOSPHORUS IN POUNDS PER ACRE, IGNITION VALUE IN PERCENTAGE

	Alabama	Maryland	Oklahoma	Central states	Chicago
Sulphur	256	460	480	600	1220
Phosphorus	90	580	694	1080	1400
Ignition value	2.194	4.53	5.528	8.00	16.05
Ratio ignition value to sulphur	182.5	196.9	230.0	263.3	263.1

life for a number of years, or have been heavily manured. Such soils would be expected to be well supplied with organic matter, and to have a correspondingly high sulphur content. If conditions are right for active sulphofication, there should be an abundance of available sulphur.

A further study has been made of this relation between the organic matter and total sulphur of the different groups of soils by determining the ratio of the organic matter to the total sulphur. As shown by table VII, this ratio is far from a constant. A 100 per cent increase in the organic matter content does not mean a corresponding 100 per cent increase in the sulphur content. A comparison of the ratios for the different groups of soils, and of the figures for the sulphur content and the organic matter content seems to justify the statement, however, that there is a general

correlation between the two, that a soil with a large amount of organic matter also contains a large amount of sulphur. That the correlation is not closer may be accounted for, at least in part, by the fact that plants differ greatly in their sulphur content. The source of the organic matter present in the soil has a great deal to do with the amount of sulphur the soil contains. This fact may account, at least partly, for the cases (shown by the tables giving the detailed data of the soil analyses) in which there does not seem to be any correlation at all between the organic matter and sulphur content. A high organic matter content may be correlated with a low sulphur content, but these cases should be considered exceptions to the general rule that a soil containing a large amount of organic matter also contains a large amount of sulphur, a rule which is seen more clearly when the sulphur and organic matter content of a number of soils are averaged. In general, the sulphur content of soils is greater than that of the corresponding subsoils.

Table VIII gives the number of crops that could be grown from the amount of sulphur present in the various groups of soils as summarized in table VII. BROWN and KELLOGG'S (2) figures for the amount of sulphur removed by maximum yields of these crops have been used. They assume that the entire crop is removed from the soil. In the Maryland and central states soils, which include the most important agricultural soils, the number of crops supply of sulphur in the poorest soil and in the best soil is given in the column "Range." Table VIII shows that there is enough sulphur present in most of the soils for comparatively few maximum crops of such high sulphur-containing plants as alfalfa and potatoes. The other crops contain less sulphur, and therefore a greater number of maximum crops of these could be grown.

Most of the sulphur of the different soils is in the organic form and unavailable for the plant, and it is not known how rapidly sulphofication is making it available. When the sulphur content of a soil is as low as it is in the Alabama, Maryland, Oklahoma, and several of the central states soils, however, sulphofication may not produce enough available sulphur to secure maximum yields of most crops. Considered from this standpoint, table VIII may

not be very significant, except as another way of comparing the sulphur content of the different groups of soils.

The sulphur content of maximum yields of the six crops given in table VIII, according to the figure of BROWN and KELLOGG, totals 134.3 pounds; the total phosphorus content 128 pounds. These are five of the most common crops, especially in the central states. Judging from the soil analyses that have been made by

TABLE VIII

NUMBER OF MAXIMUM CROPS THAT MAY BE GROWN FROM AMOUNT OF SULPHUR PRESENT IN THE FIVE SOIL GROUPS AS GIVEN IN TABLE VII

	Alabama	Maryland	Range	Oklahoma	Central states	Range	Chicago
Corn	16	28	22–37	30	37	26–72	76
Wheat	25	45	35–58	47	58	41–113	119
Oats	15	27	21–36	29	36	25–70	73
Potatoes	7	14	11–17	14	18	12–35	37
Clover	19	35	27–45	36	45	32–88	93
Alfalfa	5	10	7–13	10	13	9–25	26

various investigators, the agricultural soils of the United States are even more deficient in sulphur than in phosphorus. Although considerable sulphur is added to the soil of rainwater, a larger amount seems to be lost in drainage, some investigators stating that three times as much sulphur is lost from the soil in drainage as is added to the soil by the rain. It would seem possible, therefore, that further investigation would prove that sulphur is as generally needed as a fertilizer as is phosphorus.

EFFECT OF SULPHUR ON CHLOROPHYLL DEVELOPMENT, AND GROWTH OF RED CLOVER AND SWEET CORN

Several investigators have reported a better color in plants due to sulphur fertilization. REIMER and TARTAR (**21**), as already stated, secured greatly increased yields of alfalfa from sulphur fertilizers. They emphasize the poor color of the alfalfa on the plats not fertilized with sulphur. OLSON (**19**) speaks of the same thing in connection with experiments in Washington. The Massachusetts station (**16**) reports like results, but the beneficial effect on the color does not seem to be confined to the legumes. DULEY (**6**) reports the same thing in the case of sweet corn, and DEMOLON

(5) observed a darker green in the foliage of rutabagas, parsnips, and beets fertilized with sulphur than in the check experiments. An experiment was planned to try to determine the relation between the sulphur and the chlorophyll content of the plants. STOWELL'S evergreen sweet corn and mammoth red clover were grown in ordinary 12-inch flower pots. Thirty-six pounds of sand were added to each pot. For series 1, 2, and 3 pure quartz sand was used; for series 4, 5, 6, 7, and 8 a fine grade of torpedo sand sifted free from stones and coarse material was used. Sulphur was added to the sand, as shown in table IX. The figures in the table mean that sodium sulphate and flowers of sulphur were added in such amounts as to give the same amount of sulphur as contained in

TABLE IX

AMOUNT OF SULPHUR ADDED TO SAND CULTURES OF CLOVER AND SWEET CORN

Series	Flowers of sulphur (lbs.)	Sodium sulphate (lbs.)	Gypsum (lbs.)
1			
2		100	
3	100		
4		300	
5	300		
6		500	
7	500		
8			500

100, 300, and 500 pounds of gypsum per acre, or two million pounds of sand. Each series was run in triplicate.

The gypsum and flowers of sulphur were thoroughly mixed with the sand at the time the pots were filled. The sodium sulphate was added in solution in three applications. The corn was harvested sooner than had been planned, and received only two applications of sodium sulphate. The sodium sulphate series in the case of the corn, therefore, received two-thirds of the amount given in the table. In addition lime was added at the rate of 1000 pounds per two million pounds of sand. One week after the cultures were started 1 gm. of ferric chloride was added to the sand of each pot. The corn was planted February 7. It had previously been placed between moist filter paper, and at the time of planting all the

seeds were fully imbibed and most of them had sprouted. The clover was sown January 22, and on February 6, when the plants were 4 inches high, they were transplanted to the sand. A pure culture inoculum obtained from the Department of Bacteriology of the University of Wisconsin was added to the sand containing the clover on February 13.

The nutrient solution used was the same as that used by KRAUS and KRAYBILL (13), except that magnesium chloride was substituted for magnesium sulphate. Perhaps a solution better suited to corn and clover might have been found, but it gave good growth in both cases. It was made up as follows:

SOLUTION *A*	Per cent	SOLUTION *B*	Per cent
Magnesium chloride	2	Calcium nitrate	8
Dibasic potassium chloride	2		
Potassium nitrate	2		

Equal parts of *A* and *B* were diluted 1 to 70 with water and then mixed. The solution was applied in this strength to the corn. The solution applied to the clover was just half this strength. Five hundred cc. of these solutions were added on an average of once a week to the corn and the clover. While the plants were small and the light poor, not so much was applied, but later the supply was increased. Both the corn and clover grew well, but no marked differences in color or size of plants developed in either In fact, in the case of the corn, that in the control series was as green as the corn of any of the other series. It was not deemed the right kind of material for studying the effect of sulphur on chlorophyll development, and no chemical analyses were made.

Since no marked differences in color or growth due to sulphur deficiency had developed in the clover of the different series, it was decided to modify the experiment somewhat. It was thought the nitrate supply might be too high. On April 27 each series was divided into two parts. The nitrates were kept up in one-half of the pots and discontinued entirely in the other half, but no marked differences in color had developed at the time the experiment was stopped, on May 27. At this time the clover of the control series was somewhat paler than the clover of the high

sulphur pots, but it was not very marked. Also, no definite gradation in color from the control series to the high sulphur series was discernible. The microchemical analyses were made on the clover of the control series and the clover of the high sulphur series, in the latter case using mainly plants from series 8, the gypsum series.

The most noticeable point in table X is that the nitrates, protein, and sulphates are greater in amount in the plants of the high gypsum series. There was not much difference in the carbohydrate situation in the two series. Leaves from plants of the two series had about the same amount of reducing sugars and starch. The petioles of the control plants contained more reducing

TABLE X

MICHROCHEMICAL ANALYSES OF CLOVER PLANTS OF CONTROL SERIES AND OF HIGH SULPHUR SERIES; NITRATES DISCONTINUED MAY 27

	$CaSO_4$ HIGH			$CaSO_4$ NONE		
	Leaves	Petioles	Roots	Leaves	Petioles	Roots
Nitrates.....	+	++	++	+	+	+
Protein.....	+	++	++	+	+	+
Sulphates....	++	++	++	+	+	+
Sugar.....	+	+	++	+	++	++
Starch.....	+	++	++	+	++	+

sugar than in the case of plants from the high gypsum series, but the starch content of the petioles was about the same in both. In the roots, the reducing sugar was about the same in amount in both series, while the starch was greater in amount in the gypsum series. These differences, while clearly evident, were not great enough to permit any definite conclusions as to the relation of sulphur to chlorophyll development in the clover plant.

REIMER and TARTAR (**21**), MILLER (**18**), DULEY (**6**), and HART and TOTTINGHAM (**9**) have shown that root development and nodule formation are increased in clover and alfalfa by the use of sulphur fertilizers. PITZ (**20**) has shown that sulphur causes an increase in the nodule-forming bacteria of 2–3 fold. REIMER and TARTAR have also demonstrated that sulphur increases the nitrogen content of alfalfa 2–3 per cent. SCHERTZ (**26**) has shown

a close connection between the nitrogen and chlorophyll content of *Coleus* leaves, so that it is possible that sulphur has at least part of its effect through increasing the nitrogen content of the plant. My work seems to indicate this, but more work is desirable before coming to any definite conclusions. In the case of the non-legumes, the activity of ammonifying and nitrifying bacteria of the soil might be increased. The evidence is conflicting as to the effect of sulphur on these organisms, some claiming a favorable effect and some little effect. It is hoped to repeat this experiment, both in the case of corn and clover, omitting the nitrates entirely or keeping them very low. This should be done from the start; then, if the sulphur does have its effect indirectly by increasing the nitrogen supply through an increase in the number and activity of these organisms, this effect should be apparent. Special precautions should be taken to exclude sulphur. Sulphur-free salts, of course, should be used. The sand should be thoroughly washed with distilled water, perhaps even boiled in acid and then washed with distilled water, to eliminate any sulphur that it may contain. If decided differences in color develop, as a result of sulphur deficiency, the microchemical analyses should be followed by quantitative chemical analyses.

Table XI gives data concerning the effect of sulphur in different forms and different amounts on the growth of sweet corn. As before stated, the corn was grown with the idea of obtaining material to study the effect of sulphur on chlorophyll development in non-legumes. Since no difference in color in the different series developed, the corn was harvested and the dry weight determined, to see the effect of sulphur on the growth. It had been growing about two and one-half months and was in tassel. The details of the plan of the experiment have already been given. The numbers in the column "Treatment" indicate that flowers of sulphur and sodium sulphate were added in such amounts as to contain the same amount of sulphur as present in 100, 300, or 500 pounds of gypsum per acre, or two million pounds of sand. The percentage increase or decrease is based upon the dry weight. The minus sign indicates a decrease.

Series 4 should not be considered, for from the first the corn in two of the pots of this series did not grow well. At the time of

harvest most of this corn was short and spindling. This is believed to be due not to the sulphur treatment but to poor seed. Leaving this series out of consideration, we see that flowers of sulphur and sodium sulphate containing the same amount of sulphur as 100 pounds of gypsum, and gypsum at the rate of 500 pounds per acre gave marked increased dry weights over that of the control. The flowers of sulphur caused the greatest increase, 66.16 per cent,

TABLE XI

EFFECT OF DIFFERENT SULPHUR TREATMENTS ON GROWTH OF STOWELL'S EVERGREEN SWEET CORN IN GREENHOUSE

Series	Treatment	Moisture	Green weight (gm.)	Dry weight (gm.)	Percentage increase or decrease
1.....	Control	87.62	266.7	33.1	.....
2.....	Na_2SO_4 at rate of 100 lb. gypsum per acre	86.60	334.0	44.8	35.34
3.....	Flowers of sulphur at same rate as 2	85.12	369.6	55.0	66.16
4.....	Na_2SO_4 at rate of 300 lb. gypsum per acre	85.00	164.3	24.7	−25.37
5.....	Flowers of sulphur at same rate as 4	84.95	217.8	32.8	− 0.90
6.....	Na_2SO_4 at rate of 500 lb. gypsum per acre	85.44	222.5	32.4	− 2.11
7.....	Flowers of sulphur at same rate as 6	85.93	237.2	33.4	0.90
8.....	Gypsum at rate of 500 lb per acre.....	82.76	271.7	46.9	41.69

and gypsum was next with 41.6 per cent, sodium sulphate causing 35.3 per cent increased dry weight. It is hard to say why flowers of sulphur and sodium sulphate in the larger amounts did not bring about increased growth. The dry weight of these series is about the same as the check.

There has been work indicating injury to plants by the acid resulting from the oxidation of flowers of sulphur. Also some have claimed injury from the alkalinity developed in the soil by sodium salts. While this is a possibility, it is not emphasized. The acidity should have been taken care of by the calcium carbonate added to the sand. The literature shows that sulphur fertilization of cereals has not given consistent results, and as a rule not a very marked increased growth has been caused, so perhaps no particular significance should be attached to the fact that series 5,

6, and 7 show about the same dry weights as the check. The corn of all the series where sulphur fertilizers were used had a lower moisture content than the corn of the control series, the corn fertilized with gypsum having about 5 per cent less moisture than the control.

Summary

1. The Alabama, Maryland, and Oklahoma soils analyzed are low in sulphur, phosphorus, and organic matter; the phosphorus being not much greater in amount than the sulphur. The central states soils are better supplied, on the average, in all three respects, and decidedly better supplied with phosphorus than with sulphur. Some of these soils might be considered to have a fair amount of sulphur, phosphorus, and organic matter, while others are deficient in these respects. The Chicago soils have a fairly good content of phosphorus, and a rather high content of sulphur and organic matter. Although the sulphate sulphur content of the Chicago soils is high, this accounts for little of the total sulphur, most of it being due to the large amount of organic matter present.

2. Most of the sulphur of soils is in organic form. There is a general correlation between the sulphur and organic matter content, soils of a high organic matter content having in general a high sulphur content. The surface soils are in general higher in sulphur than the subsoils.

3. Judging from the results obtained and the work of other investigators, sulphur fertilization should prove quite generally beneficial on the Atlantic coast and the Gulf coast. The same thing may be true of the Pacific coast. Sulphur fertilizers are probably not as generally needed in the central states, many soils no doubt needing them, and many others not. Soil of a high organic matter content, such as the Chicago soils, may not need sulphur fertilizers except for high sulphur-using crops. In case the sulphate sulphur is as great in amount as it is in the Chicago soils, sulphur fertilizers might not be needed, even if the organic matter content is low. Attempts are made, in the case of several soils, to correlate the sulphur, phosphorus, and organic matter content with the production of the soils, previous treatment, or other factors.

4. No definite conclusions can be drawn from the data as to the relation of sulphur to chlorophyll development in plants. This may come about through the effect of the sulphur in increasing the nitrogen content of the plants.

5. Flowers of sulphur and sodium sulphate, containing the same amount of sulphur as 100 pounds of gypsum per acre, and gypsum at rate of 500 pounds per acre, caused increased dry weights of sweet corn of 35–66 per cent. Larger amounts of flowers of sulphur and sodium sulphate gave no increases. The corn fertilized with sulphur had a higher moisture content than the controls. In the case of the gypsum series this amounted to 5 per cent.

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EFFECT OF AUTOLIZED YEAST AND PEPTONE ON GROWTH OF EXCISED CORN ROOT TIPS IN THE DARK[1]

WILLIAM J. ROBBINS

(WITH EIGHT FIGURES)

In a previous paper[2] the writer described a simple method by which the excised root tips and stem tips of higher plants can be cultivated under sterile conditions, and some experiments in which this method was used. These experiments showed that the excised root tips of corn would make considerable growth in the dark in a sterile nutrient solution containing mineral salts and glucose, and but little when no carbohydrate was present. It was found, however, that the amount of growth which a corn root tip would make under these conditions was limited. If the original root tips were grown for ten days or two weeks in the dark in the nutrient solutions containing glucose, and then their tips cut off and transferred to fresh nutrient solutions, the amount of growth and production of secondary roots was decidedly less in the second period than in the first, and ceased entirely in the third. The following causes for this cessation of growth were suggested: (1) an unbalanced condition of the nutrient solution, (2) a deficiency of oxygen, (3) incompleteness of the nutrient solution, that is, the lack of some constituent necessary for continued growth. A consideration of the conditions of the experiments and the results obtained suggested that the third possibility should be used as a working hypothesis. This assumption does not eliminate the possibility that the cessation of growth is due to one or both of the other two factors, or that it is due to some factor not considered. It is merely used as the basis for further experimentation.

[1] Published with permission of the Director of the Agricultural Experiment Station, University of Missouri. The writer acknowledges the kindness of Dr. J. K. WILSON in supplying the Longfellow Flint corn used in this investigation, and the assistance of Dr. W. E. MANEVAL in making the transfers involved in experiments 12 and 14.

[2] ROBBINS, W. J., Cultivation of excised root tips and stem tips under sterile conditions. BOT. GAZ. **73**:376–390. 1922.

Growth of roots attached and detached from grain

That the seed supplies material different either in kind or in quantity from that present in the culture solution is evidenced by the following experiment, in which a comparison was made of the growth of roots attached to the grain and detached from the grain. In this experiment corn grains were sterilized by WILSON'S method as before, and germinated on sterile agar in Petri dishes. After germination, and when the roots were about 3 cm. long, some of the grains were placed in 50 cc. of sterile modified Pfeffer's solution plus 2 per cent glucose in 125 cc. Erlenmeyer flasks, and some of the root tips were cut off and transferred to the same kind of solution and culture flasks. All were placed in the dark at room temperature. At the end of twelve days the roots attached to the grains had gained 26.6 cm., had produced 102 secondary roots on the average, and weighed per ten roots 0.5120 gm. Those detached from the grain had gained 12.4 cm., had eighty-three secondary roots, and weighed per ten roots but 0.1138 gm. (table I).

TABLE I

GROWTH IN DARK OF ROOTS ATTACHED TO GRAIN AND DETACHED FROM GRAIN, IN PFEFFER'S SOLUTION PLUS 2 PER CENT GLUCOSE

Condition	Average original length (cm.)	Gain in length 12 days (cm.)	Average no. secondary roots	Dry weight per 10 roots (gm.)
Attached to grain	2.9	26.6	102	0.5120
Cut off	1.7	12.4	83	0.1138

In tubes of 1 per cent agar a similar difference in the growth of roots attached to the grain and detached from the grain was noted. In fig. 1 the growth of an excised root tip at the end of two weeks in modified Pfeffer's solution plus 2 per cent glucose containing 1 per cent agar, and the growth in the same period of time of a root which was left attached to the grain are shown. Comparing the latter root with the excised root, its greater length, greater size of secondary roots, and greater diameter of root tip are clearly evident.

The effect of peptone and autolized yeast

If we assume that the stoppage in growth of an excised corn root tip on continued transfers is because glucose, the mineral salts of

Pfeffer's solution, oxygen, and water are insufficient for continued root growth, the natural place to look for the materials lacking is the grain or the plant. Extracts of the young embryos including both roots and tops, and of young seedlings a week or ten days old did not benefit the excised root tips. In fact, these extracts used in the proportion of the extract of one embryo or seedling to one root tip showed a slight injurious effect upon the growth of the root.

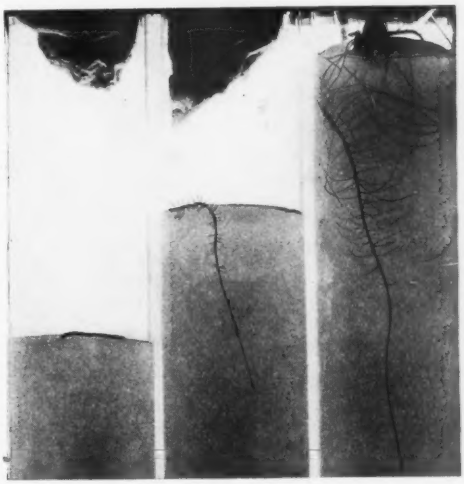

FIG. 1.—Corn root tips originally about 2 cm. long: (1) excised root tip in Pfeffer's solution plus 1 per cent agar; (2) excised root tip in Pfeffer's solution plus 1 per cent agar and 2 per cent glucose; (3) root tip of root attached to grain in Pfeffer's solution plus 2 per cent agar.

Neither did creatinine, gylcocoll, or asparagin used at the concentration of 100 ppm, 79 ppm, and 50 ppm respectively produce any better growth. The first two substances were slightly injurious, the last one no better than the check. Two experiments in which the $Ca(NO_3)_2$ and KNO_3 of Pfeffer's solution were replaced by $CaCl_2$ and KCl, and in which the roots were carried through three periods of culture, showed that the lack of nitrate somewhat decreased the total amount of growth in length instead of increasing it, as generally occurs in water cultures lacking nitrogen when the

root is attached to the grain. Peptone and autolized yeast, however, were found to be distinctly beneficial. These two substances were selected because they contained a variety of comparatively simple organic nitrogenous materials, and because they are known to be beneficial to the growth of lower plants, such as the bacteria or the yeasts.

TABLE II

EFFECT OF PEPTONE AND AUTOLIZED YEAST ON GROWTH IN DARK OF CORN ROOT TIPS CUT OFF AND TRANSFERRED

Addition to PFEFFER'S solution +2% glucose	No. roots	Average original length (cm.)	Average gain in length (cm.)	Average no. side roots	Dry weight per 10 roots (gm.)	Original P_H	Average final P_H
	1. June 21–July 4						
None	8	1.7	11.6	68	0.0487	4.5	6.8
None	8	1.7	12.7	68	0.0560	4.5	6.5
None	8	1.9	12.8	63	0.0485	4.5	6.3
	2. July 4–July 22						
None	8	1.6	2.5	8.0	0.0030	4.5	5.04
0.04% peptone	8	1.7	4.3	16.0	0.0283	6.5	6.5
0.02% yeast	8	1.7	2.2	10.0	0.0371	5.2	5.3
	3. July 22–August 20						
None	8	1.5	0.05	0	.....	4.5	4.6
0.04% peptone	4	1.8	4.1	11.0	.....	6.5	6.42
0.02% yeast	2	1.5	5.2	21.0	.....	5.2	5.45
	4. August 20–November 12						
None	.....	.....	.....	.....	.....	.....	.....
0.04% peptone	3	2.0	1.6	4.5	.....	.....	.....
0.02% yeast	1	2.0	3.5	4.0	.....	.....	.....

The first experiment with peptone and autolized yeast was begun June 21, 1920, and completed November 12 of the same year. The second experiment extended from December 13, 1920, to February 5, 1921. Both experiments demonstrated that excised corn roots whose tips were severed and transferred about every two weeks would grow in the dark in sterile solutions containing peptone or autolized yeast, glucose, and the salts of Pfeffer's solution for four to six two-week periods, while without the peptone or autolized

yeast growth stopped in the third two-week period. Autolized yeast appeared to be somewhat more favorable than peptone. The details of these two experiments are as follows.

Experiment 5.—In this experiment the method of culture was as previously described. Grains of Longfellow flint corn were sterilized by WILSON'S hypochlorite method. The excised tips of the original primary roots were grown in the modified Pfeffer's solution plus 2

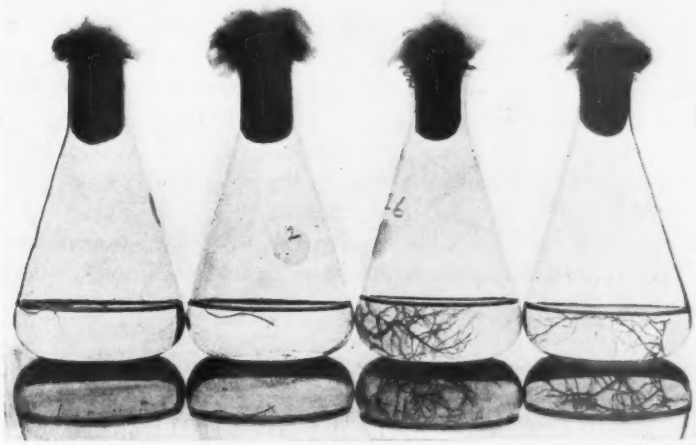

FIG. 2.—Effect of peptone at end of second period on growth of corn root tips in dark; two root tips on left in Pfeffer's solution plus 2 per cent glucose, two on right in same solution plus about 400 ppm peptone.

per cent glucose. The root tips of these excised roots were cut off after eleven days and transferred to the same solution, to the same solution plus peptone, or to the same solution plus autolized yeast. Further transfers were made as indicated in table II. Erlenmeyer flasks of 125 cc. capacity containing 50 cc. of solution were used. One cc. of a sterile 2 per cent solution of Difco peptone was added to each flask containing peptone, and 1 cc. of a sterile 1 per cent autolized yeast suspension was added to each flask containing autolized yeast. This produced solutions containing approximately

400 ppm of peptone and 200 ppm of autolized yeast. Both the yeast and peptone were sterilized intermittently at 100° C. The root tips were grown in the dark at room temperature.

The beneficial effect of the peptone and the autolized yeast began to be evident toward the end of the second period of growth. From the data in table II it can be noted that the root tips in the peptone solution show distinctly greater growth in length, production of secondary roots, and greater increase in dry weight. The maximum increase in this period in the check was 3.2 cm. with eight secondary roots, in the peptone solution 3.6 cm. with twelve secondary roots, and in the yeast 5.5 cm. with nineteen secondary roots. The appearance of two of the best root tips in the Pfeffer's solution plus glucose and in the same solution plus peptone at the end of the second period is shown in fig. 2. A number of the roots in the peptone solution, however, and still more in the autolized yeast solution developed very abnormally. They became swollen, translucent, water-soaked, and extremely brittle, and growth was stopped. From later experiments the large number of these abnormalities is believed to be due to the combined action of the peptone or yeast and the comparatively high room temperature of July (about 30° C.).

The dry weights of the root tips in the yeast and peptone solutions at the end of the second period were comparatively high, as can be noted from later experiments. These high dry weights were due to the large number of thickened and abnormal roots which developed in this period in the yeast and peptone solutions. Of the eight roots in the peptone only four were transferred, and of the eight roots in the yeast only two were transferred. These grew in the third period, however, while the check root tips did very little, as can be noted in table II. The maximum growth in the third period in the check was 0.3 cm. with no secondary roots, in peptone 7.8 cm. with twenty-nine secondary roots, in the yeast solution 9.4 cm. with forty secondary roots. The tips of three of the four roots in the peptone solution were transferred and one of the two roots in yeast. These grew in the fourth period, the maximum in the peptone being 4.5 cm. with no secondary roots, and in the yeast 3.5 cm. with four secondary roots. The one root in the yeast solution was

lost by contamination. The results of this experiment, so far as length increase is concerned, are presented graphically in fig. 3.

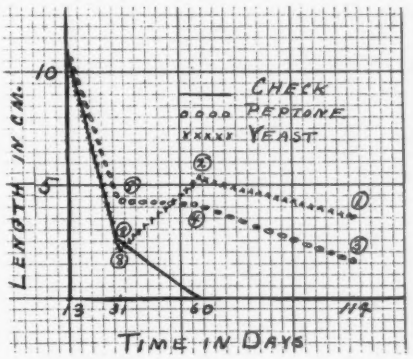

FIG. 3.—Growth in length of root tips of corn in dark for four periods; solutions used were modified Pfeffer's solution plus 2 per cent dextrose (check), and same solution plus approximately 200 ppm yeast or 400 ppm peptone; numbers within the circles represent number of root tips still growing in each period.

Determinations of the H-ion concentration of the solutions used in this experiment were made by GILLESPIE'S[3] method at the beginning and at the end of the first, second, and third periods. The modified Pfeffer's solution at the beginning of each period had a P_H of 4.5. The addition of the quantity of peptone used made the solution more alkaline, raising the P_H to 6.5. The autolized yeast had a similar though less marked effect, raising the P_H to 5.2. The growth of the roots made the check solution more alkaline (table II), raising the P_H in the first period to 6.3–6.8, in the second to 5.04, and barely affecting it in the third period. Both the yeast and the peptone exerted a buffer action, and little change in the reaction was produced in these solutions by the growth of the roots. It was noted that in the Pfeffer's solution containing glucose the change in reaction was roughly proportional to the amount of growth which the roots made. Root tips which grew but little raised the P_H from 4.5 to 5.1 in the first period; those which made the most growth raised it as high as 6.8. Higher values than this have been obtained. In one case root tips of Silver Mine corn grown for three months in the modified Pfeffer's solution plus 1 per cent cane sugar (inverted in sterilizing) changed the P_H to as high as 8.4.

Experiment 10.—In this experiment the methods followed were as in the first experiment, but two concentrations of peptone were

[3] GILLESPIE, L. J., Colorimetric determination of H-ion concentration without buffer mixtures. Jour. Amer. Chem. Soc. 42:742–748. 1920.

used instead of one. The excised primary roots of the germinated grains were grown eleven days in the modified Pfeffer's solution plus 2 per cent glucose. The tips were then cut off and transferred to the same solution, or to the same solution plus autolized yeast or peptone. Further transfers at intervals of two weeks were made, as indicated in table III.

TABLE III

EFFECT OF PEPTONE AND AUTOLIZED YEAST ON CONTINUED GROWTH OF EXCISED CORN ROOT TIPS IN DARK

Addition to PFEFFER's solution + 2% glucose	No. roots tips	Average original length (cm.)	Average gain in length (cm.)	Average no. secondary roots	Dry weight per 10 roots (gm.)
	1. December 13–December 24				
None	9	2.2	14.0	95	.....
None	13	1.9	14.2	82	.....
None	10	1.95	12.9	98.8	0.1020
None	18	1.7	12.1	72	.....
	2. December 24–January 8				
None	9	2.1	2.46	12	0.0058
200 ppm autolized yeast	13	1.9	4.8	11	0.0087
200 ppm peptone	9	2.05	2.9	16	0.0064
400 ppm peptone	14	2.1	3.7	16.7	0.0097
	3. January 8–January 22				
None	7	1.8	0.3	1.0	.....
200 ppm autolized yeast	10	2.05	2.9	4.36	0.0032
200 ppm peptone	6	1.7	0.3	2.0	.....
400 ppm peptone	12	2.0	1.4	1.6	0.0035
	4. January 22–February 5				
None	.....	.....	.....	.....	.....
200 ppm autolized yeast	9	1.6	0.83	0.65	.....
200 ppm peptone	6	1.3	0.50	0.6	.....
400 ppm peptone	11	1.7	0.28	1.0	.....

Again, toward the end of the second period of growth, the beneficial effect of the peptone and yeast was evident. In this case, however, with the lower winter temperature (ranging around 22° C. in the dark room used for incubation) the abnormalities so evident in the first experiment were not so numerous, and most of the roots were carried over into the third period. Here the check root tips again stopped growth, while those root tips in the yeast and peptone

continued to grow. They also grew in the fourth period, and of seven root tips transferred from the solutions containing autolized yeast, one grew from an original length of 1.8 cm. to 2.6 cm. in the fifth period.

It can be noted in table III and in fig. 4, where the average gains in length of the root tips in this experiment are represented graphically, that there is a continued decrease in the amount of gain in length in each successive period in both the yeast and peptone

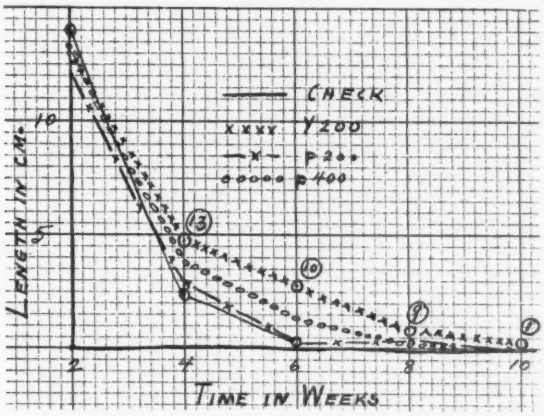

FIG. 4.—Growth in length of excised corn root tips in dark for five periods; solutions used were modified Pfeffer's solution plus 2 per cent glucose (check), same solution plus approximately 200 ppm or 400 ppm peptone (p 200, p 400) or 200 ppm of autolized yeast (Y 200); numbers within circles represent number of root tips still growing in each period in yeast extract.

solution. The decrease which occurs in the first period is the most marked. The same holds true for the production of secondary roots and for the dry weight produced in each period. The decrease is most marked in the dry weight. The dry matter produced in the second period, even in the presence of yeast or peptone, is only $\frac{1}{11}$ or $\frac{1}{12}$ of that produced in the first period. A consideration of the data of both experiments shows that autolized yeast is superior in its effect to peptone.

An observation made in this experiment as well as generally in others should be recorded. The root tips of some of the excised

roots in any series always develop abnormally. The root tip becomes clear and glassy, sinks to the bottom of the solution, and almost ceases growth. When this occurs in the early periods of an experiment the secondary roots become unusually long and well developed, frequently attaining a length three or four times that of the secondary roots of an excised root whose tip is developing normally. The appearance of a root whose primary tip became abnormal and whose secondary roots show marked development is shown in fig. 5. A normal root is shown in fig. 6. The latter figure also illustrates the fact noted before that the secondary roots develop from the convex side of the main root.

Effect of different concentrations of autolized yeast

While autolized yeast and peptone exert a favorable influence on the continued growth of the excised root tips in solution cultures containing glucose and the mineral salts of Pfeffer's solution, nevertheless the increase in length and the production of secondary roots and dry matter continuously decrease, until eventually growth stops. If we are to determine the complete nutrient requirements of a root by the method used, it will be necessary to find a set of conditions in which the excised root tips will grow continuously and produce approximately the same increase in length, number of secondary roots, and dry matter period after period as the root tips are cut off and transferred.

It was hoped that increasing the concentration of the favorable factor already found would accomplish this. Experiments were therefore carried out in which concentrations of autolized yeast varying from 10 ppm to 800 ppm were used. The results of these experiments indicated that while 400 ppm were somewhat more favorable than any of the other concentrations used, there was no marked difference in the effects of concentrations as low as 10 ppm and as high as 800 ppm so far as the growth in the early periods was concerned. In the later periods, however, the higher concentrations of yeast were more beneficial. Two experiments were performed dealing with this phase. The first extended from February 5 to April 16, the second from April 3 to May 17, 1921.

FIG. 5.—Excised corn root whose tip has developed abnormally; note development of secondary roots.

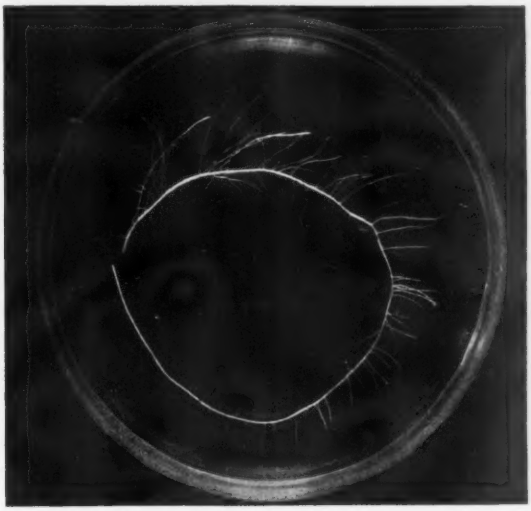

FIG. 6.—Normal excised corn root tip; compare development of secondary roots with those of root in fig. 5.

Experiment 12.—The methods used in this experiment were similar to those used in the previous experiments. The root tips were grown at room temperature in the dark in 125 cc. Erlenmeyer flasks of Pyrex glass containing 50 cc. of solution. The original excised primary roots were grown for the first period in the modified Pfeffer's solution plus 2 per cent glucose, and in the same solution plus 80, 200, 400, or 800 ppm of autolized yeast or 200 ppm of Gold Label gelatine, and transferred to fresh solutions of the same composition as in the first period. Further transfers were made as indicated in table IV. In addition, one set of root tips was grown for six weeks in the Pfeffer's solution containing 2 per cent dextrose without transferring, and one set was grown in the same solution plus 400 ppm of autolized yeast for six weeks without severing the tips, and transferring.

The autolized yeast extract used in experiment 12 was prepared by thoroughly boiling 2 gm. of autolized yeast with 100 cc. of distilled water, filtering, and making up to the original volume with distilled water. This 2 per cent extract of the autolized yeast actually contained 0.3366 gm. of dry matter per 50 cc., of which 0.0525 gm. was ash. An extract prepared in the same way was also used in experiment 14. The actual concentration of autolized yeast in the nutrient solutions to which yeast was added was about one-third of the concentrations given, which are based on the weight of the dry yeast as it came from the bottle. Table V indicates the approximate amounts of dry material, organic matter, and ash added to the culture flasks in the form of the yeast extract.

The data in table IV and the graphic representation of the lengths in fig. 7 show that during the first period the autolized yeast exerted no favorable influence on the growth of the roots. It was not until near the end of the second period that the beneficial effect of the yeast became evident. As was noted earlier, growth in the Pfeffer's solution plus 2 per cent dextrose fell off very markedly in the second period, and stopped in the third. In the presence of autolized yeast, however, the roots grew in the third and fourth periods. The number which could be transferred was decidedly reduced in the fourth period, however, but those which were transferred made some growth in the fifth period, and some of the roots

TABLE IV

EFFECT OF DIFFERENT CONCENTRATIONS OF AUTOLIZED YEAST ON CONTINUED GROWTH OF EXCISED CORN ROOTS IN STERILE CULTURE IN DARK

Addition to PFEFFER'S solution + 2% glucose	No. root tips	Average original length (cm.)	Average gain in length (cm.)	Average no. secondary roots	Dry weight per 10 roots (gm.)
	1. February 5–February 19				
None	10	1.7	12.6	67	0.0940
80 ppm yeast	10	1.8	12.0	62	0.0840
200 ppm yeast	10	1.8	11.1	60	0.0730
400 ppm yeast	10	1.9	13.0	72	0.0820
800 ppm yeast	10	1.9	11.0	56	0.0630
200 ppm gelatine	10	1.7	10.4	50	0.0624
	2. February 19–March 5				
None	9	2.3	3.0	9.6	0.0051
80 ppm yeast	10	1.9	5.97	6.1	0.0056
200 ppm yeast	10	2.16	5.71	14.0	0.0116
400 ppm yeast	10	2.0	5.4	13.2	0.0096
800 ppm yeast	10	2.1	5.5	9.0	0.0104
200 gelatine	10	1.85	2.12	3.7	0.0044
	3. March 5–March 19				
None	9	1.9	0.2	2.9	0.0015
80 ppm yeast	8	1.8	4.0	6.5	0.0035
200 ppm yeast	8	1.7	4.2	7.4	0.0043
400 ppm yeast	8	1.9	3.6	9.6	0.0055
800 ppm yeast	6	1.6	4.4	10.7	0.0110
200 gelatine	7	1.5	0.1	0	.....
	4. March 19–April 2				
None	.....	.....	.....	.....	.....
80 ppm yeast	8	2.0	1.15	2.2	0.0030
200 ppm yeast	8	1.9	1.60	0.4	0.0050
400 ppm yeast	8	1.6	1.95	3.5	0.0040
800 ppm yeast	5	1.46	2.60	5.4	0.0046
200 gelatine	.....	.....	.....	.....	.....
	5. April 2–April 16				
80 ppm yeast	3	1.5	0.7	0	.....
200 ppm yeast	4	1.35	0.5	0	.....
400 ppm yeast	2	1.65	3.3	8.5	.....
800 ppm yeast	4	1.55	0.8	3.0	.....
	February 5–March 19				
None	9	2.0	20.4	84	0.0898
400 ppm yeast	13	1.93	20.57	97	0.0635

grew in the sixth period. All the roots still growing were accidentally lost in the sixth period.

An examination of the data in table V and the curves in fig. 7 shows that none of the yeast concentrations prevented the gradual decrease in length gain, secondary root production, and dry matter

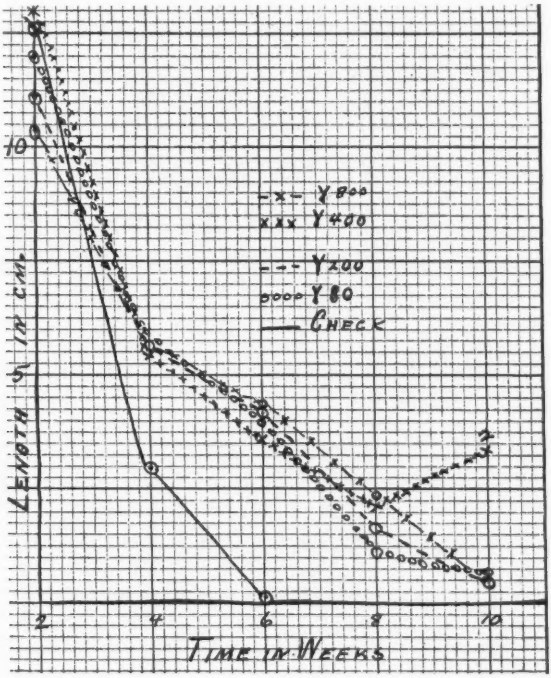

FIG. 7.—Growth in length of excised corn root tips in dark for five periods of transfers; solutions used were Pfeffer's solution plus 2 per cent glucose (check), and same solution plus 80, 200, 400, or 800 ppm autolized yeast.

elaboration. The rate of decrease was very rapid at first, but became less so as the periods passed. The increase in the rate of growth in 400 ppm of autolized yeast in the fifth period is apparent only. It is due to the fact that two roots only out of the eight of the fourth period grew in the fifth period. Their growth was excellent throughout the experiment, but decreased continuously. The

increases in length for one of these roots, no. 32, for the five periods were as follows: 11.2, 6.5, 4.9, 4.5, and 1.3 cm., and the secondary root production was 58, 12, 3, 4, and 0. For the other, no. 39, the increases in length were 13.0, 11.5, 8.3, 6.9, and 5.4 cm., and the secondary root production was 82, 51, 25, 16, and 17. These figures show a continuous decrease in length. They also emphasize the fact, which has been observed continuously in this work, that the root tips act consistently as individuals period after period. A root tip which develops well in the first and second periods usually continues to show a superior growth in the later periods.

TABLE V

APPROXIMATE ACTUAL MATERIAL, ASH, OR ORGANIC MATERIAL ADDED IN AUTOLIZED YEAST EXTRACT TO CULTURE SOLUTIONS IN EXPERIMENTS 12 AND 14

Concentrations of autolized yeast in culture solutions expressed as bottle-dry yeast (ppm)	Total dry matter (ppm)	Ash (ppm)	Organic (ppm)	Total dry matter added per 50 cc. of culture medium (gm.)
10	3.7	0.5	3.0	0.00016
40	13.5	2.0	11.5	0.00065
80	27.0	4.0	23.0	0.0013
200	67.0	10.5	56.5	0.0032
400	134.0	21.0	113.0	0.0067
800	268.0	42.0	226.0	0.0134

The difference in the effect of the various concentrations of yeast was not great, and appeared most sharply in the later periods. Thus, so far as length is concerned, the gain in 80 ppm of yeast was as great in the second and in the third period as in any of the other concentrations. The secondary root production and dry weight produced, however, were greater in the higher yeast concentrations even in the second period. It was not until the fifth period that 200 ppm of yeast showed its inferiority to 400 ppm; 800 ppm of yeast apparently was somewhat too concentrated. The addition of 200 ppm of a colloidal material like gelatine to the culture solution did not favorably affect the development of the roots. It should be noted that root hairs were found on the root tips in the gelatine solution at the end of the third period. Excised roots which did not have their root tips severed and transferred at intervals

(table VI) made just as much growth in length in a period of six weeks in Pfeffer's solution plus 2 per cent glucose as in Pfeffer's solution plus 2 per cent glucose and 400 ppm of autolized yeast.

TABLE VI

GROWTH OF EXCISED CORN ROOTS IN STERILE NUTRIENT SOLUTIONS IN DARK; IN ONE CASE ORIGINAL EXCISED ROOT TIPS NOT TRANSFERRED; IN OTHER TIPS CUT OFF AND TRANSFERRED TO FRESH NUTRIENT SOLUTIONS AT INTERVALS OF TWO WEEKS; COMPILED FROM DATA IN TABLE IV

Addition to PFEFFER'S solution	Transfers	No. roots	Average original length (cm.)	Total average gain in length (cm.)	Average no. secondary roots	Dry weight per 10 roots (gm.)
	February 5–March 19					
None	None	9	2.0	20.4	84	0.0898
400 ppm autolized yeast		13	1.93	20.57	97	0.0635
	February 5–March 19					
None	3	9–10	1.7	15.8	79.5	0.1006
400 ppm autolized yeast		8–9	1.9	22.0	94.8	0.0971

TABLE VII

EFFECTS OF 10, 40, AND 80 PPM OF AUTOLIZED YEAST EXTRACT ON GROWTH OF EXCISED CORN ROOT TIPS IN STERILE NUTRIENT SOLUTIONS IN DARK

Addition to PFEFFER'S solution+2% glucose	No. roots	Average original length (cm.)	Average gain in length (cm.)	Average no. secondary roots	Dry weight per 10 roots (gm.)
	1. April 3–April 17				
None	10	1.57	11.51	65	0.1054
None	10	1.68	11.12	64	.....
None	10	1.75	11.25	65	.....
None	10	1.68	12.22	71	0.0826
	2. April 17–April 30				
None	8	1.8	1.25	7.5	0.0027
10 ppm yeast	5	1.96	3.48	9.0	0.0047
40 ppm yeast	3	1.9	2.5	6.0	.....
80 ppm yeast	3	2.0	2.8	2.0	.....
	3. April 30–May 14				
None	8	1.4	0.13	0	.....
10 ppm yeast	5	1.8	1.5	1.2	.....
40 ppm yeast	2	1.8	1.5	0	.....
80 ppm yeast	2	1.6	1.1	0	.....

The secondary root production in the autolized yeast culture was somewhat greater and dry matter somewhat less in this case.

If we compare the growth of roots which had their tips severed and were transferred twice to fresh solutions during a six weeks' period with those which grew continuously undisturbed in the solution, we find (table VI) that in Pfeffer's solution plus 2 per cent glucose the total increase in length and production of secondary roots when the tips were severed and transferred was less than when they were left undisturbed; the dry matter was greater. When yeast was present the length and secondary root production were not affected by the transfers; the dry weight was greater.

The original P_H of the Pfeffer's solution plus 2 per cent glucose was 4.5. The roots which grew for six weeks without transfer changed the reaction to P_H 6.3. The original reaction of the Pfeffer's solution plus 2 per cent glucose and 400 ppm of yeast was P_H 5.2. The roots which grew for six weeks without transfer changed the reaction to a P_H of 6.24.

Experiment 14.—The methods and general conditions were the same in this experiment as in experiment 12. In this case, however, concentrations of yeast of 10, 40, and 80 ppm were used. The root tips were grown for the first period with no addition to the nutrient solution, the yeast being added in the second period. Unfortunately one of the flasks containing the concentrated yeast extract was contaminated with bacteria, and most of the cultures were lost in the second period due to the contamination, leaving but two root tips in each of the concentrations, 40 ppm and 80 ppm. From the data in table VII and the graphic representations in fig. 8 it can be noted that the

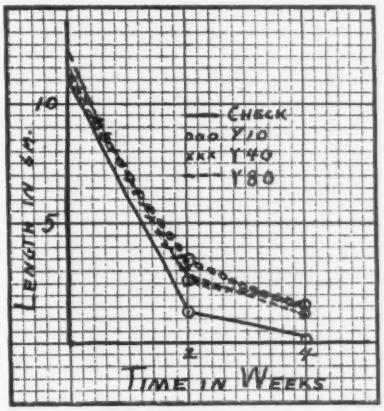

FIG. 8.—Growth in length of excised corn root tips in dark for three periods of transfers; solutions used were Pfeffer's solution plus 2 per cent glucose, and same solution plus 10, 40, or 80 ppm of autolized yeast.

growth in 10 ppm of autolized yeast in the second period compares very favorably with that in 40 ppm or 80 ppm of yeast in the same experiment. In the third period the development in the solution containing 10 ppm of autolized yeast was better than in either 40 or 80 ppm of yeast. If, however, we compare it with the previous experiment in which a larger number of root tips were grown in 80 ppm yeast, we can see that the development was considerably less in 10 ppm than in 80 ppm of yeast. This substantiates the general expression of the effect of autolized yeast in these experiments, namely, that in the first period it has no beneficial effect, in the second period there is little difference between the effects of 10, 40, 80, 200, 400, and 800 ppm; but the later the period the more evident does the beneficial action of the higher concentrations appear.

Discussion

While excised corn root tips which are grown in the dark for about two weeks in Pfeffer's solution plus 2 per cent glucose, and which have their root tips cut off and transferred to fresh solutions at intervals of two weeks, show a continued decrease in the rate of growth and stop growth in the third period, the addition of small amounts of peptone or autolized yeast permits them to grow for as long as six periods before growth ceases.

Two possible explanations for the action of the peptone and autolized yeast suggest themselves: (1) the autolized yeast or the peptone supplies something which the root requires for its continued growth and which is not included in the salts of Pfeffer's solution, water, glucose, and free oxygen; (2) the autolized yeast or peptone balances the solution, performing a function which could be accomplished by a readjustment of the relative quantities of the salts of Pfeffer's solution or their equivalents, of water, of glucose, and of free oxygen. A definite decision between these two possibilities cannot be made from the data at hand. The majority of the results reported in this paper, however, would seem to be explained best on the assumption that the mineral salts of Pfeffer's solution, glucose, free oxygen, and water are insufficient for the continued growth of the root cells of corn, and that this deficiency can partially be supplied by autolized yeast or peptone.

That the effect of the peptone or autolized yeast is not protective is indicated by the fact that a colloidal material like gelatine is not beneficial, and by the fact that the beneficial action of the yeast does not appear in the first period of two weeks, or even in six weeks when the excised roots do not have their tips cut off and transferred to fresh solutions. The assumption, however, that the seedling root contains some substance or substances derived from the grain which are not contained in the basic nutrient solution and which are supplied by the peptone or autolized yeast would explain: (1) That root tips transferred show less total growth than those not transferred. The hypothetical materials are fractionated in the transfers, and the transferred root is limited in the second and third periods by a deficiency of these materials, which can partially be supplied by the peptone and autolized yeast. (2) That in the presence of autolized yeast root tips transferred show as much growth as those not transferred. The hypothetical substances fractionated in the transfers are supplied by the autolized yeast. (3) The fact that with the cessation of growth of the root tip of an excised root there occurs an excessive development of secondary roots. The hypothetical materials which are not used in the growth of the main root tip are utilized for growth by the meristematic tissue of the secondary roots.

Whatever the cause of the beneficial action of the autolized yeast,[4] its effect is limited in some way, as is evidenced by the fact that the various concentrations of yeast produce no correspondingly increased benefits, and the Pfeffer's solution containing peptone or autolized yeast and glucose will not permit continued growth.

Summary

1. Corn roots attached to the grain grow much more rapidly under sterile conditions in the dark in Pfeffer's solution plus 2 per cent glucose than do root tips detached from the grain.

[4] Lack of space precludes a summary at this time of the voluminous literature dealing with this general problem. Reference should be made to the publications of SACHS, HABERLANDT, HANNIG, BOTTOMLEY, WEBER, BACHMAN, LOEB, MOCKERIDGE, FULMER, NELSON and SHERWOOD, WILLIAMS, and others who have dealt previously with the problem of the necessity of accessory food substances for plant growth, or who have attempted to cultivate single cells or isolated parts of higher plants. Some of the more recent papers on this subject not cited in the earlier publication by the writer are given at the end of this paper. A review of the subject indicated is planned for a later publication.

2. When excised root tips of corn are grown under sterile conditions for about two weeks in the dark in Pfeffer's solution plus 2 per cent glucose, and their root tips are severed and transferred to fresh solutions at intervals: (*a*) growth stops in the third period; (*b*) the addition of peptone or autolized yeast permits the root tips to grow for 4–6 periods; (*c*) a concentration of 200 ppm of gelatine, 100 ppm of creatinine, 79 ppm of glycocoll, 50 ppm of asparagin, or the corn embryo extract used show no beneficial effect; (*d*) in Pfeffer's solution lacking nitrates and containing 2 per cent glucose a little less total growth is made than in Pfeffer's solution containing nitrates and 2 per cent glucose; (*e*) approximately 400 ppm of peptone is more efficient than 200 ppm; (*f*) autolized yeast is more beneficial than peptone; (*g*) the beneficial effect of the autolized yeast does not appear in the first period of growth; (*h*) concentrations of 10, 40, 80, 200, 400, and 800 ppm of autolized yeast (equivalent in dry matter to about one-third the concentrations given) show no marked difference in their beneficial effect, especially in the early periods; (*i*) the higher concentrations of yeast evidence a somewhat greater beneficial effect in the later periods than the lower concentrations.

3. When the total growth of excised corn root tips whose tips are cut off and transferred twice in a six weeks' period is compared with that of root tips left undisturbed, then (*a*) in Pfeffer's solution plus 2 per cent glucose in the dark the total growth in length and production of secondary roots are less, the dry weight is greater; (*b*) in Pfeffer's solution plus 2 per cent glucose and 400 ppm of autolized yeast there is no difference in the growth in length or secondary root production; the dry weight is greater.

4. When the growth of excised root tips left undisturbed for six weeks in Pfeffer's solution plus 2 per cent glucose is compared with the growth in the same solution to which 400 ppm of autolized yeast is added, there is no difference in total length. The secondary root production is somewhat less and dry weight somewhat greater.

5. Excised corn root tips act as individuals.

6. The growth of the secondary roots of an excised root is much greater when the primary root tip stops growth than when it continues to grow normally.

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LEAVES OF THE FARINOSAE[1]

AGNES ARBER

(WITH PLATES I–III)

Introduction

In papers published in this and other journals during the last few years (ARBER 1–10) I have dealt with the results of the application of the phyllode theory to the leaves of various groups of monocotyledons. The present paper discusses, from this standpoint, the leaf structure of the families associated by ENGLER (11) in the cohort Farinosae. Examination of this group is a matter of some difficulty to a British botanist, since the eleven families which it includes are represented in Europe by one species alone, *Eriocaulon septangulare* With., and even in cultivation comparatively few genera belonging to these families are to be found. I have thus been unable to carry this study so far as I should have wished, because it has been necessary to rely almost entirely on limited quantities of herbarium material, which, in the case of the many fibrous-leaved members of the Farinosae, is peculiarly intractable to sectioning. MCLEAN'S (14) method of preparing dried material has proved invaluable, however, even in the case of plants which have lain in herbaria for many years. The specimen of *Cephalostemon affinis* Koern., for instance, sections of which are represented in fig. 26 *A–C*, was collected by SPRUCE in South America as long ago as 1853.

I am indebted for material to the Director of the Royal Botanic Gardens, Kew; the Keeper of the Department of Botany, British Museum (Natural History); Mr. L. RODWAY, of Hobart, Tasmania; and Professor A. C. SEWARD.

I propose in the first place, taking the families in the order in which they appear in ENGLER'S *Pflanzenfamilien*, briefly to describe the principal types of leaf met with in the cohort, and then to discuss their interpretation.

[1] This paper represents part of the work carried out during the tenure of a Keddey Fletcher-Warr Studentship of the University of London.

Flagellariaceae

I hope to describe the leaves of this family in a later paper, so I will omit all discussion of them here; their most unusual feature is that, in the genus *Flagellaria*, they have tendril apices.

Restionaceae

In this family, which consists of nineteen genera, plants with radical leaves are rare. The genus *Anarthria*, however, forms a notable exception, for it has basal leaves recalling those of *Iris*, which may either be ensiform or "radial." Fig. 3 *A* represents the transverse section of the limb of *Anarthria scabra* R.Br. It will be seen that it has a type of anatomy resembling that of an *Acacia* phyllode, the bundles, which are in two series lying to right and left of the median plane of the leaf, having their xylems directed inward. The palisade parenchyma is interrupted at very short intervals by bands of fibers, one of which occurs between each of the main bundles and the epidermis, while others are associated with the smaller bundles, or occur independently. Fig. 3 *B* shows the margin of such a leaf, with the median bundle, on a larger scale. Two of the fibrous bands (*f*) are visible, and it will be seen that, in the marginal region, the palisade parenchyma passes over into thick-walled elements without contents. The epidermal cells also increase in size and in the thickness of their sclerised walls as the margin is approached. Fig. 4 *A–C* shows the leaf of *Anarthria gracilis* R.Br., which, instead of being ensiform like that of *A. scabra*, is radial. The limb (*C*), in which the fibrous sheaths of the bundles with their extensions to the epidermis form a conspicuous feature, is almost cylindrical in section. The leaves of *Anarthria*, however, are not typical for this family, in which it is usual to find cauline leaves alone. Such leaves generally have a well developed sheath, succeeded by a relatively unimportant limb, which may be flattened or cylindrical, but is often reduced to a mere point (examples occur in *Dovea*, *Elegia*, *Lepyrodia*, and a number of other genera). Fig. 1 *A* shows the appearance of the leaf of *Restio tremulus* R.Br. It has a sheathing base (*s*) which more than surrounds the axis, forming a "wrap-over." The same peculiarity in other members of this family may be carried to a further point; in a species of

Thamnochortus, the sheathing base of the scale leaf is described by VELENOVSKÝ (**18**) as surrounding the axis spirally, and, according to his fig. 358, its attachment forms more than two complete turns round the axis. Both sheath and narrow, flat limb of *Restio tremulus* are fibrous (fig. 1 *B*, *C*), and toward the apex of the limb there is a marked increase in the lignified and sclerised tissue (fig. 1 *D*). The leaf of *Leptocarpus peronatus* Mast., with its sheathing base and limb reduced to a mucro, is represented in fig. 2. In the case of *Elegia deusta* Kth. the leaf apex is more solid, and includes a ring of bundles (**10**, fig. 5 *A*, *B*).

Centrolepidaceae

The leaves of the Centrolepidaceae are usually small, with a sheathing base and an awl-like or threadlike limb. *Gaimardia australis* Gaudich. (fig. 5 *A–C*) may be taken as an example. There is a sheathing leaf base and an awl-like limb, traversed by three bundles inclosed in fibrous sheaths. The leaves of this family may be of a more reduced type, however, as in *Centrolepis aristata* R. and S. In this plant I have found one bundle, traversing both sheath and limb (fig. 11 *B*, *C*). GOEBEL (**13**), on the other hand, describes and figures the leaf anatomy of this species as belonging to an extremely reduced ensiform type, with a second bundle above the median bundle, resulting from the fusion of two laterals. Although I have not found this structure in the only two foliage leaves which I was able to examine, I have seen it in two of the bracts from the base of the inflorescence (*b*, fig. 11 *A*). These bracts are well developed structures with a sheath and limb, closely resembling the foliage leaves.

Mayacaceae

The very delicate leaves of the single aquatic genus *Mayaca*, of which this family consists, are traversed by a single vascular strand (fig. 27 *A*). Several species figured in the *Flora Brasiliensis* (**17**) have a bifid leaf apex, such as is shown here for *M. fluviatilis* Aublet (fig. 27 *B*). It will be seen that the vascular bundle (*vb*) takes no part in the bifurcation, but terminates below the fork.

Xyridaceae

This family consists of two genera, *Xyris* and *Abolboda*. *Xyris*, which includes about forty species, has a leaf with a sheathing base and an ensiform limb, recalling that of many members of the genus *Iris*. In *Xyris Wallichii* Kth. (figs. 12 *A–C*) and *X. brevifolia* Mich. (fig. 18 *A*, *B*) the single bundles alternate to right and left in the flattened limb. Fig. 18 *B* shows the marginal strand of *Xyris brevifolia*, which is peculiar in the possession of a conspicuous mass of fibers adjoining the bundle on the xylem side, whereas such a fibrous strand is more usually developed outside the phloem. As POULSEN (**16**) has already shown, the vascular bundles of the leaves of *Xyris* may either be single or associated in groups of two or more. Figs. 13 and 14 show bundle groups in the case of *X. asperata* Kth. (*trachyphylla* Mart.) and *X. anceps* Lam. These bundle groups may attain considerable complexity; that represented in fig. 13 *B* (*X. asperata*) consists of nine strands imbedded in a common fibrous sheath. Although the flattened ensiform leaf type is usual in *Xyris*, it is not universal. POULSEN (**16**) has figured a species (*X. teretifolia* Poulsen) in which the transverse section of the leaf limb is oval, the distance between the adaxial and abaxial margins being only about half as much again as the width.

In *Xyris* the leaf epidermis is generally thick-walled. It may retain much the same character at the two margins as on the flanks of the leaf (*X. Wallichii*, fig. 12 *C*), or the elements at the margins may be considerably elongated, forming a fibrous border to the leaf (*X. anceps*, fig. 14 *B–D*). In this case the marginal elements, instead of standing out horizontally, slope downward, with the result that they are cut obliquely in transverse sections passing through the leaf border, which at first glance thus suggest that the epidermis is multi-layered in this region (fig. 14 *D*).

Xyris gracilis R.Br. is significant as possessing sheathing leaves, in which the limb may be reduced to a mere point, and in which the leaf base forms practically the whole organ (fig. 17). These leaves may be compared with those of the second genus of Xyridaceae, *Abolboda*. I have examined the leaves of *A. grandis*

Griseb. var. *minor*, and find them to be traversed by a single series of normally orientated bundles, corresponding to those in the sheath leaves of *Xyris gracilis* (fig. 17 *C*). *A. Poarchon*, as figured by SEUBERT (**17**), has an acuminate apex to the foliage leaf, while it also has bracts which terminate in a "cornet," recalling that described by HALLIER in the case of the sepals of certain dicotyledons (see reference and discussion, **10**). It is probable that the apex in both foliage leaf and bract of *A. Poarchon* Seub. is a vestigial petiole, and is morphologically equivalent to the ensiform limb of *Xyris*.

Eriocaulaceae

The Eriocaulaceae have both cauline and radical leaves of a simple type. The two principal genera are *Eriocaulon* and *Paepalanthus*, both of which include more than a hundred species. Fig. 19 *A* shows the general internal structure of the British species of *Eriocaulon*, *E. septangulare* With. A large proportion of the leaf is occupied by lacunae, separated by lamellae, each of which includes a single normally orientated bundle. Fig. 19 *B* shows one lamella with its vascular strand on a larger scale. A fragment of a diaphragm (*d*) with intercellular spaces between its cells is seen attached to the lamella on one side. In *E. cuspidatum* Dalz. the limb terminates in a mucro (fig. 19 *D*), while in *E. Wallichianum* Mart. f. *submersa* the tip of the ribbon leaf is minutely truncate (fig. 19 *C*). In this aquatic species, as in so many water plants, there is an increase of the tracheal tissue near the leaf apex, and there are indications of water stomates and possibly an apical opening, but in herbarium material it is difficult to identify these structures with certainty. The leaves of certain species of *Eriocaulon* may be much reduced; in the aquatic *E. setaceum* L. the fragile linear leaf, traversed by a single bundle, recalls that of *Mayaca*. In the case of *Paepalanthus* I have examined one species, *P. speciosus* Gardn. Here, as in *Eriocaulon*, there is one series of normally orientated bundles in the leaf. The large epidermal cells are a striking character.

Rapateaceae

The leaves of this family are much larger and more complex than those of the Eriocaulaceae; they may show a definite differ-

entiation into sheath, petiole, and limb (*Rapatea longipes*, fig. 24). A curious feature common to the leaves of various members of the family is their tendency to asymmetry. The leaf sheath, as ENGLER points out in the *Pflanzenfamilien*, is folded, but the median bundle does not occupy the trough of the fold, and the limb correspondingly is not of equal width on either side of the midrib. These features are shown in fig. 24, *Rapatea longipes* Spr.; fig. 25 *A*, *B*, *R. angustifolia* Spr.; and fig. 26 *A*, *B*, *Cephalostemon affinis* Koern. In the last species the sheath is peculiar, since it thins out markedly at the fold, which is quite remote from the median bundle, whose position is marked externally by a ridge of fibrous tissue (*f*) adjacent to the lower surface (fig. 26 *A*). This ridge can also be recognized in the limb (fig. 26 *B*). The lacunate character of the leaf tissue in *Rapatea angustifolia* Spr. is indicated in fig. 25 *C*, which also shows the median bundle with its fibrous sheath, and the small fibrous strands which run beneath the epidermis. The details of the median bundle of the limb of *Cephalostemon affinis* are seen in fig. 26 *C*.

Bromeliaceae

The leaves of the Bromeliads are often of a simple type, with a broadly sheathing base prolonged into a linear to ovate limb. In some cases, however (*Tillandsia usneoides* L. fig. 20 *A*, *B*), there is a marked distinction between the sheathing leaf base and the limb, which has a definitely petiolar character. In other cases the main part of the leaf suggests a leaf base, but there is a solid apical region which may correspond to the limb of *Tillandsia usneoides* on a reduced scale (10). The figures of *Aechmea gamosepala* Wittm. in the *Flora Brasiliensis* (15) show that the foliage leaves in this case have an acuminate apex, while the outer perianth members terminate in an elongated mucro, which is probably equivalent to the "cornet" in the case of *Abolboda Poarchon* Seub., discussed in a preceding paragraph.

Commelinaceae

The leaves of this family differ from most of those hitherto considered in their very complete differentiation. They usually

have a conspicuous sheath, sharply marked off from a limb, from which it may or may not be separated by a distinct petiolar region. Fig. 9 represents the leaf of *Streptolirion volubile* Edgw., in which all these parts are well developed. In *Commelina*, *Aneilema*, and *Tradescantia* there is a striking range of form in the limb, which in different species shows (within each genus) gradations from linear to ovate.

Pontederiaceae

Fig. 8 *A* represents what is perhaps the most complex type of leaf met with in the Farinosae, that of *Eichhornia speciosa* Kth. (*Pontederia crassipes* Mart.). The ligular sheath (*lig. s*, fig. 8 *A*, *B*) with its lobed apex, almost suggesting a second leaf blade, to which attention has been drawn by GLÜCK (**12**), is, as he points out, unparalleled among monocotyledons; it may perhaps be remotely compared with the curious frill-like top of the ochrea of a *Polygonum* from Java, figured by VELENOVSKÝ (**18**, fig. 277). The petiole of *E. speciosa* is dilated, and terminates in a limb, which, as shown in a previous paper (**1**), possesses both normal and inverted bundles (fig. 8 *C*). In this paper it was recorded that inverted bundles occurred in the limb of *Eichhornia*, *Pontederia*, and *Heteranthera*. The family also contains three other genera, *Monochoria*, *Reussia*, and *Hydrothrix*. In *Monochoria plantaginea* Kth. I have now been able to observe that inverted as well as normal strands occur, and in a very small fragment of the leaf of *Reussia subovata* Solms, the only material available from this genus, I again found both types of strand. It has thus been possible to establish the occurrence of inverted strands in five genera of the Pontederiaceae; the sixth, *Hydrothrix*, is an aquatic plant in which it is useless to look for this anatomical peculiarity, since, as GOEBEL has shown, the leaf is so much reduced as to be traversed by one vascular strand alone (**1**).

The shape of the limb in the Pontederiaceae ranges from the narrow, almost linear form sometimes met with in *Monochoria plantaginea*, to broader types with a cordate base, such as *Pontederia nymphaefolia* Kth., or with an auricled base, such as that illustrated in *M. hastaefolia* Presl (fig. 7).

Philydraceae

This small family consists of four species assigned to three genera. Sections were secured of three of these species, one belonging to each genus. The monotypic *Philydrum lanuginosum* Banks (fig. 22) has an ensiform leaf, whose shape and plan of vascular anatomy recall *Anarthria scabra* R.Br.; the leaf, however, is conspicuously lacunate. *Pritzelia pygmaea* F. Muell., representing the second of these monotypic genera, is related to *Philydrum* in its leaf structure, very much as *Anarthria gracilis* is related to *A. scabra*. The leaf of *Pritzelia* has a sheathing base (fig. 21 *A*) and a limb, which so closely approximates to radial structure that it is not possible to determine from internal evidence which is the median bundle (fig. 21 *B*). The leaf contains a number of large, solitary, acicular crystals (*c*, fig. 21 *C*). The leaves of the third genus, *Helmholtzia*, have been described as equitant and ensiform, but Dr. STAPF has been so kind as to inform me that in both the two species of which the genus consists, *H. acorifolia* F. Muell. and *H. glaberrimum* Hook. f., the vaginal portion of the leaf is strongly keeled, and that this keel runs as a midrib throughout the "vertical" limb. The limb is thus expanded in a plane at right angles to the truly ensiform limb of *Philydrum*. In accordance with this difference of construction, the leaf anatomy of the species which I have been able to examine, *H. acorifolia*, proves to be dorsiventral, with palisade parenchyma on the adaxial surface (fig. 23 *A*, *B*). The most striking feature of the leaf from the present standpoint is that, despite its dorsiventrality, it is characteristically phyllodic in structure, containing, besides normally orientated bundles (*nb*), others that are inverted (*ib*). Fig. 23 *C* shows the inverted group from the upper side of the midrib, in greater detail.

Conclusions

CLASSIFICATION OF LEAF TYPES IN FARINOSAE

In the preceding pages the treatment of the leaves of this cohort has been almost exclusively descriptive, but I propose now to consider the interpretation of their morphology. The most

concise way is probably by means of a classification, based on the phyllode theory, of the principal types of leaf enumerated in dealing with the various families. On this basis the leaves of the Farinosae fall into the following six groups:

1. Phyllodes consisting of a sheathing base, and an ensiform limb equivalent to a petiole flattened in the vertical plane; for example, *Anarthria scabra* R.Br. (Restionaceae), fig. 3; *Xyris* (many species) (Xyridaceae), figs. 12, 14, 18; *Philydrum* (Philydraceae), fig. 22.

2. Phyllodes consisting of a sheathing base, and a limb departing little in character from a normal petiole and containing an arc or ring of bundles; for example, *Anarthria gracilis* R.Br. (Restionaceae), fig. 4; *Elegia deusta* Kth. (Restionaceae) (**10**, fig. 5 *A*, *B*); *Gaimardia australis* Gaudich. (Centrolepidaceae), fig. 5; *Xyris teretifolia* Pouls. (Xyridaceae) (**16**, fig. 3); *Pritzelia pygmaea* F. Muell. (Philydraceae), fig. 21.

3. Phyllodes essentially similar to (2), but in which the petiolar limb is reduced to a mere point; for example, *Leptocarpus peronatus* Mast. (Restionaceae), fig. 2; *Eriocaulon cuspidatum* Dalz (Eriocaulaceae), fig. 19; some Bromeliaceae.

4. Phyllodes similar to (3), but further reduced until they consist of leaf bases alone; for example, many Eriocaulaceae and Bromeliaceae.

5. Phyllodes in which the whole or the distal region of the petiole is flattened in the horizontal plane into a pseudolamina, containing inverted as well as normal bundles; for example, Pontederiaceae (figs. 7, 8); *Helmholtzia acorifolia* F. Muell. (Philydraceae), fig. 23.

6. Phyllodes in which the whole or the distal region of the petiole is expanded in the horizontal plane to form a pseudolamina without inverted bundles; for example, many Commelinaceae; *Rapatea* (Rapateaceae), figs. 24, 25.

Comparison with leaves of other cohorts

One of the most striking results elicited by a general study of monocotyledonous leaves is the way in which certain leaf types recur again and again in this group, among plants by no means closely allied to one another. The leaves of the Farinosae afford many examples of these parallelisms. I will confine myself to an attempt to trace some of the relations between the leaf types of

the Farinosae and those of two other cohorts, Helobieae and Liliiflorae; the Liliiflorae include those monocotyledons most nearly related to the Farinosae (11), while the Helobieae are somewhat more remote.

The ribbon leaves of certain aquatic species of *Eriocaulon* recall the leaves of a corresponding form met with so frequently among the Helobieae (7), although, if my interpretation be correct, the ribbon leaves of Helobieae are of petiolar nature, while in those of *Eriocaulon* merely the leaf base is represented. Although the proportion of the parts is so different, it is such a leaf as that of *Restio tremulus* (fig. 1 *A*), rather than that of a submerged *Eriocaulon*, which is equivalent to the ribbon leaf of, for instance, *Cymodocea nodosa* of the Potamogetonaceae (7). On the other hand, those leaves of the Farinosae in which the limb, although linear, is rather awl-like than ribbon-like, such as *Tillandsia usneoides* (Bromeliaceae, fig. 20), and *Gaimardia australis* (Centrolepidaceae, fig. 5), may be closely compared with *Cymodocea manatorum* (7). The venation of the limb of *Streptolirion volubile* of the Commelinaceae again (fig. 9) resembles that of *Alisma parnassifolium* (7). A contrast with the Helobieae, however, is furnished by *Monochoria hastaefolia* (fig. 7), whose venation is essentially different from those of the species of *Sagittaria*, which it recalls in the outline of its pseudolamina (7). Turning to more detailed structure, the inverted bundles in the leaf limb of the Pontederiaceae and of *Helmholtzia* find their analogue in those of certain Hydrocharitaceae.

The occurrence of the ensiform leaf in the Farinosae, both in the Restionaceae, Xyridaceae, and Philydraceae, is another instance of the widespread distribution of this leaf type among the monocotyledons. It is known from the Helobieae, Spathiflorae, Liliiflorae, and Microspermae, as well as in the Farinosae. Not only in form, but also in internal structure, this type of leaf shows remarkable uniformity in the different groups. *Xyris Wallichii* (fig. 12 *A*) and *X. brevifolia* (fig. 18 *A*), with their alternating bundles, can be paralleled in *Iris* (1, 6). The fibrous margins, also, which are so marked a feature of the ensiform leaves of many Liliiflorae (6), reappear in *Xyris*. For comparison with the leaves

of the Farinosae, fig. 6 *A* and *B* show a section of the ensiform limb of *Hewardia tasmanica* Hook. (Liliaceae). It will be seen that in the distribution of the marginal fibers it resembles both *Tritonia* (fig. 10), and *Xyris Wallichii* (fig. 12 *C*) and *X. anceps* (fig. 14 *D*). This similarity is also carried into the details of the vascular system. Fig. 6 *A* shows examples from the limb of *Hewardia* of opposite bundles imbedded in a common fibrous sheath, and thus resembling the pair of bundles from the limb of *Xyris montivaga* Kth., shown in fig. 15. With this may also be compared the paired bundles of *Tofieldia* of the Liliaceae (**1**), *Tetroncium* of the Juncaginaceae (**7**), and *Tritonia* (fig. 16 *A*, *B*) and *Moraea Robinsoniana* (**6**). These bundle pairs are not only characteristic of the ensiform leaves of monocotyledons, but may be found also among the *Acacia* phyllodes, with which I believe these leaves to be homologous; they occur, for instance, in *Acacia neurophylla* (**6**). In addition to these bundle pairs, which clearly originate by more or less complete fusion of strands belonging to the opposite sides of the phyllode, *Xyris* also shows bundle groups of a different nature, illustrated here in the case of *Xyris asperata* (fig. 13 *A–C*) and *X. anceps* (fig. 14 *A*). These find their parallel in the tribe Johnsonieae of the Liliaceae (**5**). In the limb of *Arnocrinum Drummondii* Endl. there are bundle groups imbedded in fibers, which may be compared with those of *Xyris asperata*. It is true that they do not, as in the case of *Xyris*, occur in an ensiform leaf, but the ensiform leaf type is found in *Johnsonia*, to which *Arnocrinum* is probably more nearly related than it is to the five other members of the tribe.

The Farinosae furnish additional evidence for the close relationship of the ensiform and "radial" types of leaf. This relation, to which attention has already been called, both in the case of the leaves of the Liliiflorae and of the phyllodes of *Acacia*, is displayed with special clearness in *Iris*, among whose species there are examples of both forms of leaf, and also of intermediate types. In the Restionaceae, Xyridaceae, and Philydraceae there are comparable cases. Within the genus *Anarthria* both types are found (cf. figs. 3 and 4), and the same is true of *Xyris* (cf. figs. 12, 14, 18 with POULSEN'S fig. 3 of *X. teretifolia*, **16**); while the ensiform

leaf of *Philydrum* (fig. 22) may be compared with the "radial" leaf of the related genus *Pritzelia* (fig. 21).

The type of leaf consisting of a sheathing leaf base terminating in a more or less cylindrical apex, which I interpret as a reduced petiole, occurs both in the Farinosae and Liliiflorae. For instance, the leaf of *Elegia deusta* Kth. (Restionaceae) is closely similar to that of *Distichia clandestina* Buch. of the Juncaceae (10). The apical tendril of *Flagellaria* (Flagellariaceae) also recalls that of *Gloriosa* and other Liliaceae. I hope to discuss the morphology of these leaf tendrils in a later paper.

To complete the parallel between the leaves of the Farinosae and those of the Liliiflorae, it may be noted that the limbs of the Pontederiaceae and of *Helmholtzia*, with their inverted bundles, to some extent approach those of certain species of *Allium* (5), and of such Amaryllids as *Zephyranthes* (8); while the similarity in shape of the cordate leaf limb of the Commelinaceous climber, *Streptolirion volubile* (fig. 9), and that of various Dioscoreaceae and Liliaceae is of wider interest, since it is an example of the recurrence of a form which appears again and again among monocotyledons. In former papers (1, 4) I have brought together a number of instances, from this class, of leaves with a cordate base; the list of families in which leaves of this type are found may now be increased to ten by the addition of the Stemonaceae, Amaryllidaceae, and Hydrocharitaceae. This comparison between the leaves of the Farinosae and those of the Helobieae and Liliiflorae emphasizes again the important part which parallelism of development has played in the evolution of the monocotyledonous leaf. The tendency for related stocks (even those whose affinity is far from close) to progress along corresponding lines is no doubt a very general feature of evolutionary history, although its prevalence is only gradually receiving full recognition. The fact that, in the monocotyledonous leaf, such parallelisms are displayed to an almost exaggerated degree, becomes to some extent explicable, if this organ is regarded as a phyllode consisting of leaf base and petiole alone. The loss of the lamina would inevitably impose restrictions upon the further evolution of the leaf, by confining its potentialities within a narrowed boundary. It might thus

induce a tendency to the repetition of a definite series of forms, monotonous in the basic features of their construction, but endlessly varied within their given limits.

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EXPLANATION OF PLATES I–III

Throughout, xylem (*xy*) shown in black; phloem (*ph*) in white; and fibers (*f*) dotted; *lac*, lacuna; *pp*, palisade parenchyma; *mb*, median bundle;

ep, epidermis; *s*, sheath; *pet*, petiole; *l*, limb; *n*, node; *ax*, axis; in all sections of equitant leaves, the identity of abaxial and adaxial margins has had to be decided on internal evidence, owing to fragmentary character of herbarium material available.

PLATE I

FIG. 1 *A–D.—Restio tremulus* R.Br.: *A*, axis bearing leaf (×½); *B*, transverse section sheath of leaf (×14); *C* and *D*, transverse section limb of another leaf (×23); *D* nearer apex than *C*.

FIG. 2.—*Leptocarpus peronatus* Mast., axis bearing leaf (×½).

FIG. 3 *A*, *B.—Anarthria scabra* R.Br.: *A*, transverse section leaf limb (×14), section slightly reconstructed at upper margin; *B*, dorsal (abaxial) margin of *A* (×77).

FIG. 4 *A–C.—Anarthria gracilis* R.Br., transverse section one leaf: *A*, sheath (section slightly reconstructed at margins of sheath); *B*, basal part of limb; *C*, limb (×23).

FIG. 5 *A–C.—Gaimardia australis* Gaudich.: *A*, leaf (×3½ circa); *B* and *C* transverse section of one leaf (×77); *B*, sheath; *C*, limb.

FIG. 6 *A*, *B.—Hewardia tasmanica* Hook. (for comparison): *A*, transverse section leaf limb (×23); *B*, upper margin of *A* (×77).

FIG. 7.—*Monochoria hastaefolia* Presl, limb of leaf to show venation (×½).

FIG. 8 *A–C.—Eichhornia speciosa* Kth.: *A*, small leaf to show dilated petiole and ligular sheath (*lig.s*) (×½); *B*, top of sheath from *A*, viewed from adaxial side to show three ligular lobes (×½); *C*, transverse section through margin of leaf limb in *A*, in direction of arrow (×14); *nb*, normally orientated bundles; *ib*, inverted bundles.

FIG. 9.—*Streptolirion volubile* Edgw., axis bearing leaf (×½).

FIG. 10.—*Tritonia*, garden hybrid (for comparison), margin of ensiform leaf (×193).

FIG. 11 *A–B.—Centrolepis aristata* R and S.: *A*, axis of small plant bearing inflorescence inclosed in bracts (*b*, *b*), foliage leaf to right (×½); *B*, transverse section sheath foliage leaf (×23); *B*, transverse section limb (×77); *bs*, bundle sheath, consisting of one inner thick-walled layer, and one outer layer of larger cells with thinner walls.

PLATE II

FIG. 12 *A–C.—Xyris Wallichii* Kth.: *A*, transverse section leaf limb (×23); *B*, stomate from *A* (×198); *C*, margin of *A* (×198).

FIG. 13 *A–C.—Xyris asperata* Kth. (*trachyphylla* Mart.): *A*, transverse section transition region between sheath and limb (×23) to show bundle groups; *B*, bundle group marked *x* in *A* (×77); group of four bundles (b_1, b_2, b_3, b_4), in common fibrous sheath, from transverse section of leaf limb (×318).

FIG. 14 *A–D.—Xyris anceps* Lam.: *A*, transverse section limb of leaf (×23); b_1, single bundle; b_2, group of two bundles; b_3, group of three bundles; *B*, apex of leaf limb viewed as solid object (×23); *C*, fibrous margin of leaf viewed as solid object (×77); *D*, transverse section margin of *A* (×77).

FIG. 15.—*Xyris montivaga* Kth.: pair of opposite bundles (xy_1 and ph_1, xy_2 and ph_2) in common fibrous sheath (×318); similar to b_2 in fig. 14 *A* (*X. anceps*).

FIG. 16 *A*, *B*.—*Tritonia* (garden hybrid) for comparison, lettering as in fig. 15; fibers represented in black (instead of white with double lines indicating thickness of walls, as in other figures): *A*, pair of opposite bundles from transverse section of leaf limb (×318); *B*, similar pair of bundles, but with xylems fused (×318).

FIG. 17 *A–C*.—*Xyris gracilis* R.Br.: *A*, leaf consisting mainly of leaf sheath, with reduced limb (*l*); *B*, apex of another reduced leaf in which limb is absent (both natural size); *C*, transverse section of leaf shown in *B* (slightly enlarged).

FIG. 18 *A–B*.—*Xyris brevifolia* Mich.: *A*, transverse section leaf limb (×23); *B*, marginal bundle such as that marked *x* in *A* (×193).

FIG. 19 *A–D*.—*Eriocaulon: A* and *B*, *E. septangulare* With.; *A*, transverse section of limb of leaf (×23); *B*, lamella marked *x* in *A* (×77); *ue*, upper epidermis, *le*, lower epidermis; *d*, fragment of diaphragm seen in surface view; *C*, *E. Wallichianum* Mart. f. *submersa*, apex of leaf (×½); *D*, *E. cuspidatum* Dalz., apex of leaf to show mucro (×½).

FIG. 20 *A*, *B*.—*Tillandsia usneoides* L., transverse section leaf (×23): *A*, sheath; *B*, limb.

PLATE III

FIG. 21 *A–C*.—*Pritzelia pygmaea* F. Muell., transverse section leaf: *A*, sheath; *B*, limb (×23); orientation of *B* uncertain; *C*, margin of sheath in *A* (×77) to show stomate (*st*) and crystals (*c*).

FIG. 22.—*Philydrum lanuginosum* Banks, transverse section limb of leaf (×14).

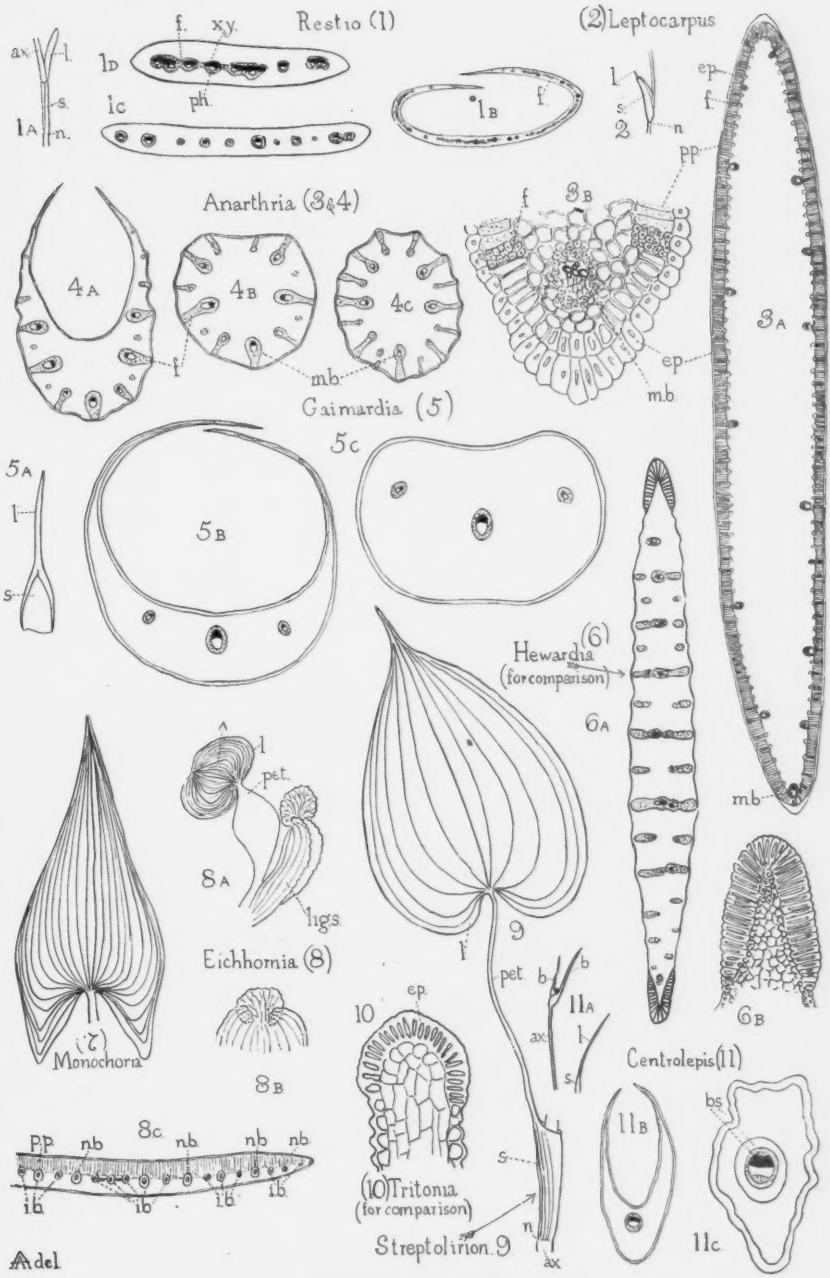
FIG. 23 *A–C*.—*Helmholtzia acorifolia* F. Muell., *A* and *B*, transverse section limb of leaf (×23): *A*, midrib region (*mr*); *B*, margin, to show normally orientated bundles and bundle groups (*nb*) and inversely orientated bundles and bundle groups (*ib*); *C*, inverted bundles of midrib from section similar to *A* (×77).

FIG. 24.—*Rapatea longipes* Spr., small leaf (×½).

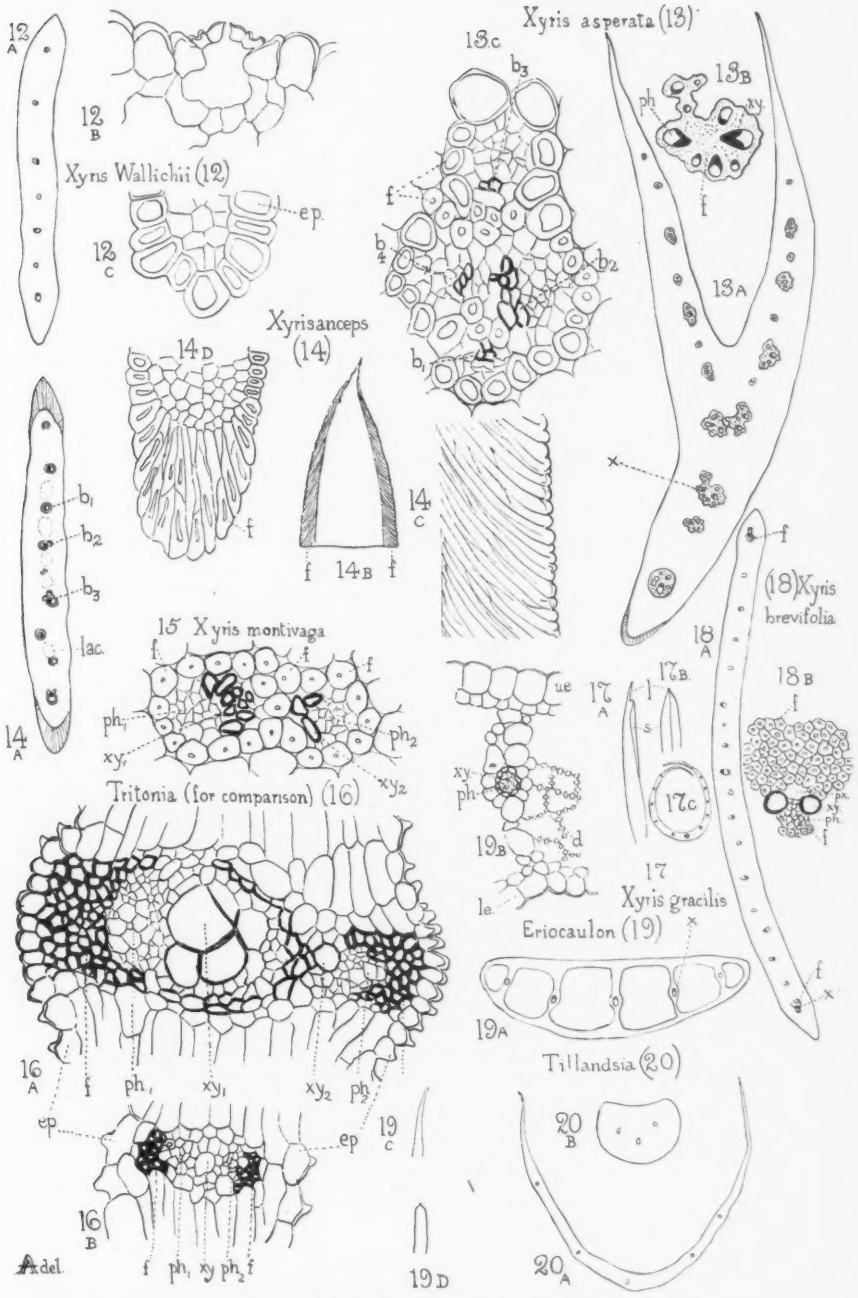
FIG. 25 *A–C*.—*Rapatea angustifolia* Spr.: *A* and *B*, transverse section leaf (×14); *A*, sheath; *B*, limb; *C*, median bundle (*mb*), of limb in *B* (×77).

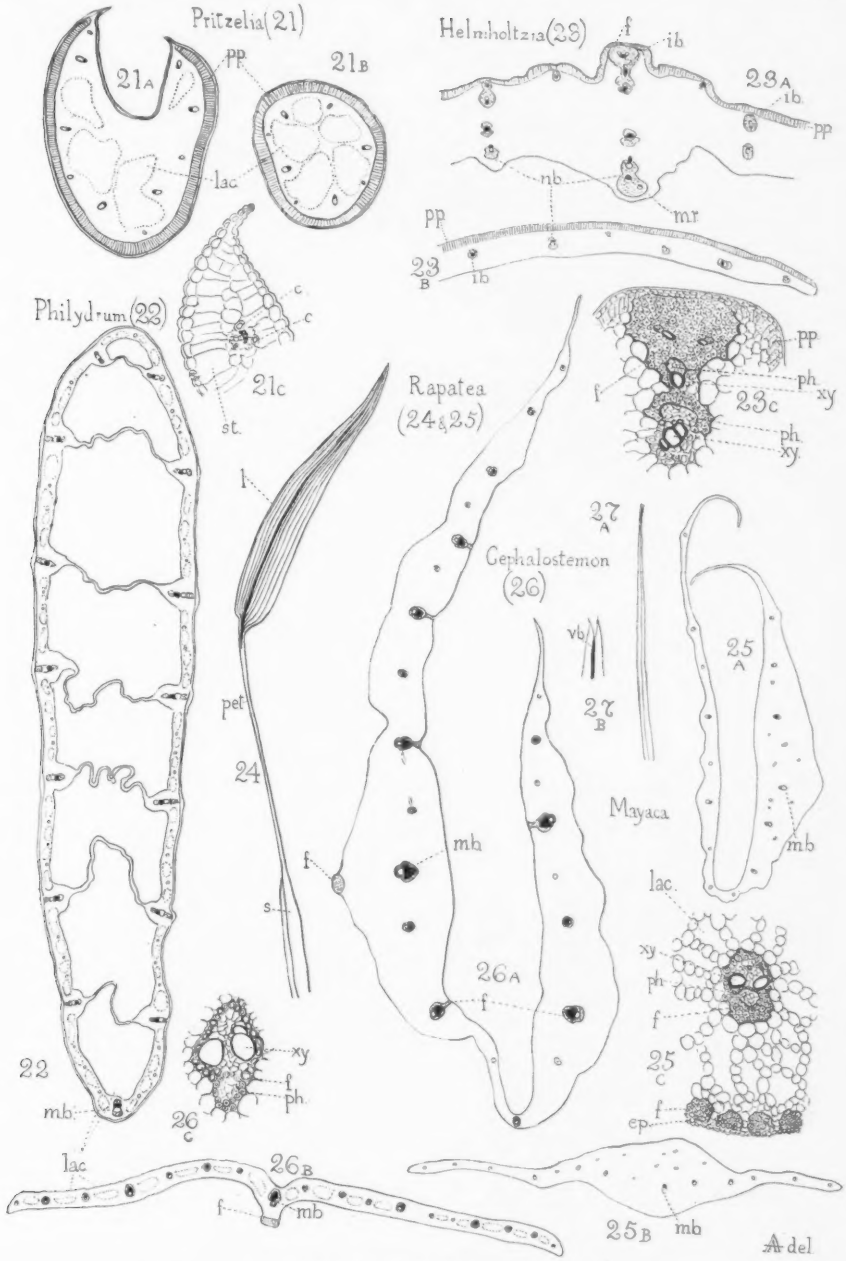
FIG. 26 *A–C*.—*Cephalostemon affinis* Koern: *A*, *B*, transverse section leaf (×14); *A*, sheath; *B*, limb; *C*, median bundle of limb (×77).

FIG. 27 *A–B*.—*Mayaca fluviatilis* Aubl.: *A*, leaf (×½); *B*, leaf apex (×14); *vb*, vascular strand.



ARBER on FARINOSAE


Xyris asperata (13)
Xyris Wallichii (12)
Xyrisanceps (14)
15 Xyris montivaga
Tritonia (for comparison) (16)
Eriocaulon (19)
Xyris gracilis
(18) Xyris brevifolia
Tillandsia (20)
ARBER on FARINOSAE



ARBER on FARINOSAE

INHERITANCE OF FRUIT SHAPE IN CUCURBITA PEPO. I

EDMUND W. SINNOTT

(WITH THREE FIGURES)

During the past few years much progress has been made in our knowledge of the inheritance of quantitative characters. We know much less, however, about the factors which control the interrelationships between these various size characters, and which thus determine the shape of the organism. The present paper is a preliminary report on some investigations dealing with certain phases of shape inheritance in the summer squash.

For the past six seasons the writer has been carrying on some breeding work with a number of the common types of *Cucurbita Pepo*. Commercial material of this species is apt to be very much hybridized and consequently to yield a remarkable variety of forms. Many strains are also self-sterile, or become so after a year or two of inbreeding. A considerable variety of types was obtained from four leading seed firms in the spring of 1916, and an attempt was made, by persistent self-fertilization, to establish from this highly heterozygous material types which would be essentially pure. Of course the majority of plants refused to set seed under these conditions, but about twenty-five were found which were self-fertile, and the offspring of these (except for a number of lines which have since been lost through sterility) have been continuously inbred for six generations. In most cases sterility disappeared by the fourth generation, and by this time such a high degree of uniformity was shown in all plant characters as to make it clear that a fairly close approach to homozygosity had been attained. In 1919 a number of crosses involving all the more notable character differences were made among these various pure types, and the uniformity of the F_1 in every case gave further assurance that the parent types were approximately pure. An F_2 generation from each of these crosses was made during the past season (1921).

A number of the pedigrees involved rather radical shape differences in the original types crossed. Several pure strains of the ordinary "scallop" or "pattypan" type were obtained (fig. 1) with fruit essentially disclike in shape, being from two to four times as broad as thick, with the teeth or scallops around the edge varying in number, shape, and development. In one race of white discs there appeared very early several plants in which the fruit differed markedly from that of the disc parent, being nearly spherical in shape, approximately as thick as broad, and with a rather weak development of teeth. Intermediate forms did not appear, and the spheres when inbred never produced any other shape. Several pure lines with spherical fruits were thus obtained (fig. 1).

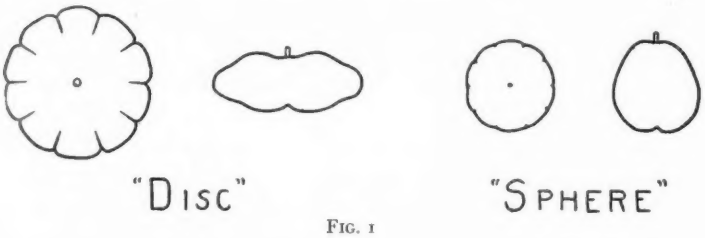


FIG. 1

A single plant of one of these spherical-fruited lines was crossed in 1919 with a plant from each of three disc-fruited lines. These three lines differed somewhat in fruit shape, one having a relatively flat disc and the others relatively deep ones, one being somewhat flatter than the other. The F_1 generation in each case showed complete dominance of the disc shape, and the type of disc (deep or flat) was essentially like that of the particular disc parent used. In the F_2 generation there was a sharp segregation into approximately three-quarters disc and one-quarter sphere. It is evident that the chief difference between these two shapes is caused by a single factor, and that this shows complete dominance. F_2 counts for the three pedigrees, together with the results expected on the single factor hypothesis, are shown in table I.

The problem is not quite so simple as this, however, for the F_2 segregates do not resemble exactly the original types, it being especially noticeable that the sphere segregates differ in shape, those

coming from the crosses where the flattest disc was used being noticeably flatter than those coming from the crosses where the thickest disc was used.

TABLE I

FRUIT SHAPE IN F_2 OF THREE CROSSES OF DISC×SPHERE

Pedigree	Disc	Sphere
15	83	18
1	79	29
19	41	13
Total	203	60
Expectation, 3:1	197	66

To bring out more clearly the various shape differences, a study of the relative sizes of the two major dimensions, width and length, as represented by an index, is useful. This shape index for a given fruit is its width (the dimension at right angles to the fruit axis) divided by its length or thickness (dimension parallel to the fruit axis). The means for the shape index of parents, the F_1, and the two extracted types in the F_2 for the three pedigrees, are set forth in table II. The frequency distribution of the individuals in the three pedigrees with respect to this shape index is also given in fig. 2.

TABLE II

MEANS FOR FRUIT SHAPE INDEX (WIDTH÷LENGTH) IN THE FOUR PURE LINES STUDIED, IN F_1 AND THE TWO TYPES SEGREGATING IN F_2, FOR THE THREE PEDIGREES; FIGURES IN PARENTHESES ARE INDICES EXPECTED ON BASIS OF TWO-FACTOR HYPOTHESIS

Pure lines	Observation	Expectation	F_1	Observation	Expectation	F_2	Disc		Sphere	
							Observation	Expectation	Observation	Expectation
103 (sphere)	0.97	.....								
15 (disc)	2.48	(2.47)	15	2.59	(2.47)	15	2.51	(2.47)	0.86	(0.97)
1 (disc)	2.50	(2.72)	1	2.91	(2.72)	1	2.61	(2.66)	1.20	(1.16)
19 (disc)	3.28	(3.22)	19	3.34	(3.22)	19	2.94	(3.03)	1.50	(1.53)

Records for a comparatively small number of individuals of the four pure types are here presented, since only a few plants are grown of each of the various pure lines in any one year. The F_1 generations were also small, but the F_2 generations were considerably larger. Cultures involving much greater numbers are now being grown.

From a study of these few individuals, however, certain points stand out clearly. The F_1 shows complete dominance of the disc shape. In fact, in every case the F_1 is even a little flatter than the parent disc. This is notably the case in pedigree 1, but there is reason to believe that the pure type of this line is probably a little flatter than is shown by the individuals here portrayed.

In pedigree 15, which involves the deepest disc, both the sphere and disc F_2 segregates are essentially like the original types, being a little deeper in each case. A single factor difference between disc and sphere is apparently sufficient to account for these facts. It will be noted that there is a very sharp segregation between the two shapes in the F_2. In pedigree 19, however, which involves the flattest disc, the F_2 spheres are decidedly flatter than the parent sphere type (1.50 as compared with 0.97), and the F_2 discs distinctly deeper than the parent disc type (2.94 as compared with 3.28). Pedigree 1 is somewhat intermediate between these, the F_2 spheres being somewhat flatter than the original sphere type, and the F_2 discs being about the same as the original disc type, but considerably deeper than the F_1 discs.

In pedigrees 19 and 1 there is evidently something more than a single disc or "flattening" factor at work. This coincident flattening of the spheres and deepening of the discs may readily be explained by assuming that there is a second dominant flattening factor, considerably weaker in its effect than the major one already discussed, and segregating independently of it. The parent disc type would possess both of these and the parent sphere type lack them both. The major difference between disc and sphere would still be caused by the larger factor, the "spheres" lacking it and the "discs" possessing it. In the F_2, however, three-quarters of the spheres would possess the smaller flattening factor, and the average shape of the whole sphere group would thus be flatter than that of the pure type; and a quarter of the discs would lack this smaller factor and thus be less flat than the original discs in which both flattening factors are present. This would tend to bring the two shape types somewhat nearer together in the F_2 than in the pure types, a condition which evidently obtains in these two pedigrees.

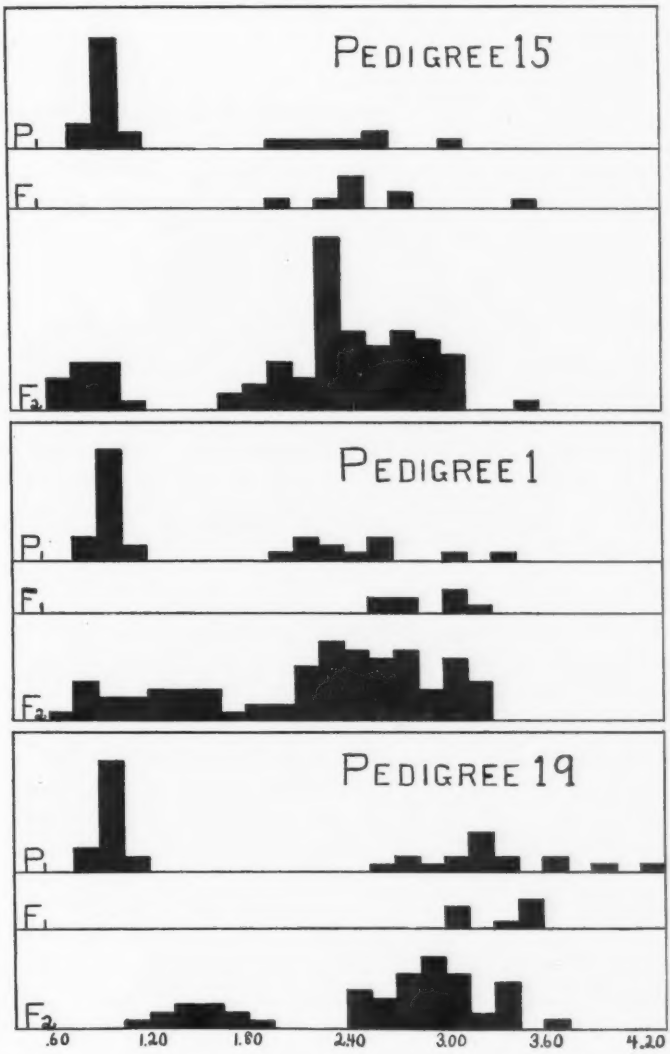


FIG. 2.—Fruit shape index (width/length) in parents, F_1 and F_2 of three pedigrees

If we assume that the discs used in pedigree 15 differ from the spheres by the possession of a single dominant flattening factor *A*, which increases the index by 1.50, that in pedigree 19 the disc type possesses in addition to this a second dominant flattening factor *B*, which increases the index by 0.75, and that in pedigree 1 the supplementary flattening factor (which we may call *C*) is smaller and can increase the index by only 0.25, we would obtain approximately the shapes which we actually find in the F_2. The original sphere type has an index of 0.97. The disc in pedigree 15 would thus have an index of 0.97 plus 1.50, or 2.47, as compared with the 2.48 which was found. The F_1 and F_2 types would be expected to repeat these indices, a condition which they come reasonably close to doing. In pedigree 19, however, the parent disc (*AB*) would have an index of 0.97 plus 1.50 plus 0.75, or 3.22, as compared with the 3.28 observed. The F_1 should be approximately the same. In the F_2 three-quarters of the spheres would be *aB*, 0.97 plus 0.75, and the other quarter *ab*, 0.97 only, giving a mean for the whole sphere group of 1.53. Similarly, three-quarters of the discs would be *AB* or 3.22, and one-quarter *Ab* or 2.47, giving a mean for the disc group of 3.03. These indices are close to the actual figures. The same general situation would occur in pedigree 1, factor *C* being present instead of *A*, and the original disc type being *AC*. In table II the actual indices and the theoretical expectations are both presented.

It will be noted that this hypothesis does not explain the fact that the F_1 discs are in every case flatter than the pure types. The numbers involved are also much too small to prove such a hypothesis. They certainly seem to indicate, however, that in two of the disc types more than one factor is responsible for the shape difference between it and the sphere, and that these two factors are of unequal effect.

This is probably a rather simple case of shape inheritance. Indeed, other pedigrees at present in process of completion indicate that shape inheritance in squashes is often much more complex, involving a considerable number of factors, some of which also show lack of dominance. In GROTH'S[1] work with tomatoes, a

[1] GROTH, B. H. A., Some results in size inheritance. N.J. Agric. Exp. Sta. Bull. 278. pp. 92. *pls.* 34. 1915.

study of the F_2 in a number of crosses involving differences in fruit shape shows that a distinct bimodal curve is present, thus suggesting a segregation something like that here reported in squashes. In many other shape crosses studied by this investigator, however, the F_2 showed a wide range of shapes with no clear cut segregation of

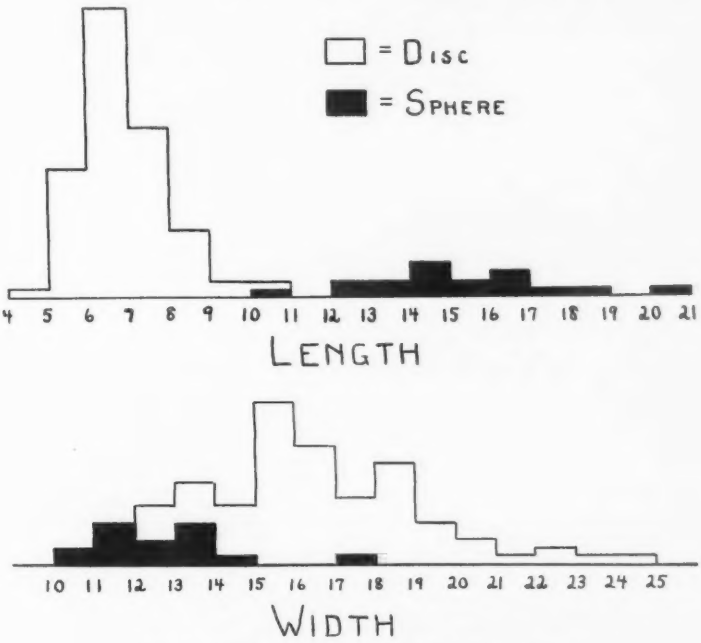


FIG. 3.—Length and width of F_2 fruits, pedigree 19

types, thus suggesting the operation of a larger number of factors. EMERSON'S[2] work with squashes also shows a great increase in the variability of shape in the F_2 and (apparently) no clear cut segregation. The parental types used by EMERSON, however, were not inbred homozygous strains.

It is assumed that in the present case such things as "shape factors" exist in the germ plasm and are operative. It may be objected

[2] EMERSON, R. A., The inheritance of sizes and shapes in plants. Amer. Nat. 44:739–746. 1910.

that the results are due merely to a segregation of those size factors which control fruit thickness and fruit width. That such an explanation is scarcely tenable, however, is indicated by a study of the actual dimensions in the F_2, for here we find that the squashes which are the longest (thickest) are also those which are narrowest (thus producing the sphere types), and that the squashes which are thinnest are also those which are widest (thus producing the disc types). The frequency distribution of the actual lengths and the actual widths of the F_2 fruits in pedigree 19 are set forth in fig. 3. That part of each curve which consists of individuals which are spherical in shape is shaded, the discs remaining white. In fruit length there is evidently a fairly clear segregation into long and short, but no segregation is apparent in width. It is noteworthy, however, that the long fruits are not scattered irregularly through the various widths, as would be the case if length and width segregated independently, but that in practically all cases these long fruits are considerably narrower than the average, and the short fruits wider than the average, so that instead of a great variety of types in two rather vague groups, two very distinct shapes result.

There is evidently something controlling the dimensional proportions which the individual exhibits, and thus determining its shape. The relation between these shape factors and those which control size is a matter of considerable interest. The suggestion is perhaps worth considering that the ordinary "size" factors govern in some way the total amount of growth attained, and that the shape factors control the distribution and proportions of this growth.

Summary

1. Pure lines of summer squashes differing in fruit shape have been isolated.

2. In crosses between a type with approximately spherical fruits and three different races having "scallop" or "disc" fruits, the disc shape showed complete dominance in the F_1 in every case, and in the F_2 there was a sharp segregation into three-quarters disc fruits and one-quarter sphere. A single, large, dominant flattening factor thus seems to distinguish these disc types from the spherical ones.

3. In two of these crosses, the extracted spheres are distinctly flatter than the pure types, and the extracted discs distinctly deeper than the pure discs. This can be explained by assuming the operation, in each case, of a second flattening factor, also dominant, but showing a much smaller effect than the first.

4. Evidence is brought forward that shape-determining factors actually exist, and that the facts here set forth are not due merely to the segregation of size factors.

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BIOCHEMISTRY OF PLANT DISEASES[1]

IV. PROXIMATE ANALYSIS OF PLUMS ROTTED BY SCLEROTINIA CINEREA

J. J. Willaman and F. R. Davison

(with two figures)

In the third paper of this series (6) the literature bearing on the chemistry of plant diseases, especially the effect of disease on the composition of plants and the chemical differences between resistant and non-resistant varieties of the same species of plant, was reviewed in some detail. Since the present work is a continuation of the former, it will not be necessary to make reference again to the results of other investigations, except incidentally during the discussion.

In the previous work on the brown rot of plums, caused by the fungus *Sclerotinia cinerea*, it was found that during the progress of the rotting the H-ion concentration of the sap increases markedly; that oxalic acid is produced, but hardly in sufficient quantity to account for the increased acidity; that tannin decreases during the rotting; that protein nitrogen increases, due probably to the protein formed in the fungus mycelium. Resistant varieties did not differ conspicuously from non-resistant varieties, so far as the analyses showed, except that the resistant varieties usually had a more acid sap, and that more oxalic acid was produced in them. The tannin content of green plums usually increases after picking from the tree, but infection by *Sclerotinia* entirely inhibits this increase.

Experimentation

In the present work the ordinary proximate analyses, together with the determination of calcium, were made, using four varieties of plums at three stages of maturity, grown at the University Fruit

[1] Published with the approval of the Director as Paper no. 272, Journal Series, Minnesota Agricultural Experiment Station. Presented at the meeting of the American Chemical Society, September 9, 1921.

Breeding Farm at Excelsior in 1918.[2] In table I are given the data concerning the samples.

PREPARATION OF MATERIAL.—The plums were halved or quartered, freed from the pits, and placed in ovens at about 90°–95° C. until dry enough to grind. It was not thought necessary to use special precautions in drying, considering the nature of the analyses to be made. The finely ground material was stored in bottles. The plums were rotted by sterilizing in mercuric chloride solution, and then inoculating with a suspension of spores by means

TABLE I

DATA ON PLUM SAMPLES, 1918

Lab. no.	Variety	Abbreviation	Date picked	Stage of growth	Condition of fruit	No. of days required for rotting	Texture of rotted fruit
	Resistant						
79...	Burbank×Wolf 9	B×W 9	July 2	I	Green, half grown	9	Firm
87...	Burbank×Wolf 9	B×W 9	Aug. 21	II	Fully grown, not ripe	12	Firm
91...	Burbank×Wolf 9	B×W 9	Sept. 3	III	Ripe	10	Fairly firm
80...	Abundance×Wolf 18	A×W 18	July 2	I	Green, half grown	12	Firm
88...	Abundance×Wolf 18	A×W 18	Aug. 21	II	Fully grown, not ripe	9	Hard
92...	Abundance×Wolf 18	A×W 18	Sept. 3	III	Ripe	11	Firm
	Non-resistant						
81...	Compass	C	July 2	I	Green, half grown	6	Soft
89...	Compass	C	Aug. 2	II	Fully grown, not ripe	7	Soft and watery
93...	Compass	C	Aug. 8	III	Ripe	6	Soft
82...	Sand cherry×Formosa	SC×F	July 2	I	Green, half grown	6	Somewhat soft
90...	Sand cherry×Formosa	SC×F	Aug. 2	II	Fully grown, not ripe	7	Soft
94...	Sand cherry×Formosa	SC×F	Aug. 8	III	Ripe	6	Soft

of a hypodermic syringe, plunging the needle right to the pit. It required from eight to fourteen days for complete rotting, as shown by the tissue becoming dark brown throughout.

METHODS OF ANALYSIS.—The moisture content of each sample was carefully determined at the time the other analyses were made, by drying to constant weight in a vacuum at 60° C. For the ash determination, 2 gm. samples were incinerated in platinum dishes, and then heated in a muffle at 550° C. until constant in weight. The calcium was determined in the ash by the MCCRUDDEN method (3), which has proved to be very simple and accurate. The Official Methods (1) were followed for total nitrogen and ether extract,

[2] The writers' thanks are due to Dr. M. J. DORSEY for his courtesies in furnishing the samples.

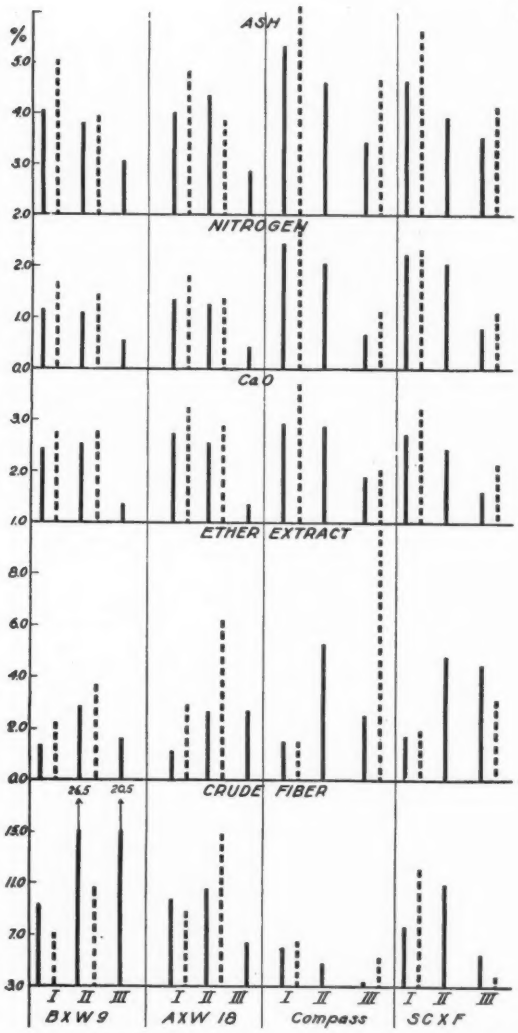

FIG. 1.—Composition of sound and of rotted plums of various varieties at three stages of growth: solid line, sound samples; dotted line, rotted samples; see table I for stages of growth and names of varieties.

and the KENNEDY (2) modification of the SWEENEY method was used for crude fiber.

Results

The data obtained in these analyses are shown graphically in figs. 1 and 2. All values are calculated to a moisture free basis. In fig. 1 the sound and rotted portions of each sample are placed side by side, so as to show the change in composition during rotting. It will be seen that in almost all cases the rotted portion shows a higher content of all constituents except crude fiber; the latter shows no general tendency in either direction, sometimes being greater and sometimes less in the rotted than in the sound material. The increase in these constituents is probably due to loss of dry matter through respiration. Previous work has shown that respiration is higher in infected than in sound plums, and this results in a relative increase in the substances determined. The figures for ether extract and for crude fiber are erratic in their changes, which is in keeping with the empirical nature of the methods of analysis.

In fig. 2 the same data are used, but they are arranged so as to give more direct comparison of varietal characteristics. The first

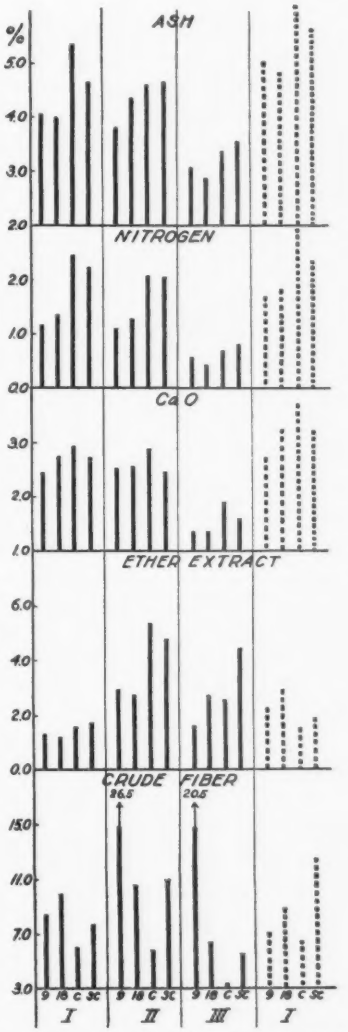

FIG. 2.—Composition of sound and of rotted plums, grouped to bring out varietal differences: solid line, sound samples; dotted line, rotted samples; first two varieties in each group are resistant to brown rot; second two are susceptible; see table I for stages of growth and names of varieties.

two varieties in each section, indicated by 9 and 18, are resistant; the next two are non-resistant. Some of the rotted samples are missing, due to loss by contamination. It will be seen that the crude fiber is markedly higher in the resistant than in the non-resistant varieties, but all other constituents are lower. This relation holds in both the sound and the rotted samples, although data for the latter are available for the first stage only. VALLEAU (4) reports a positive correlation between firmness of the plum flesh and its resistance to brown rot. The firmness is due to the structural elements of the tissue, the cellulose cell walls and the pectic middle lamellae. Only the former are represented in the determination of crude fiber. From the results at hand it appears quite probable that the quality and quantity of cellulose material are important factors in resistance properties, although the pectic substances also play a part in the metabolism of this fungus, as was pointed out in a previous paper of this series (5). In what ways the middle lamella may play a part in resistance properties is not known. Since it is a compound of pectin with calcium, it was thought that determinations of calcium in the present samples might throw some light on the question, but the data show that calcium is higher in the susceptible varieties in about the same magnitude as the ash and nitrogen, and no special significance can be seen in it.

In fig. 2 can be seen certain changes in the composition of plums during the course of ripening. As maturation progresses, the ash, nitrogen, and calcium steadily decrease. This is probably due to large increases in the soluble carbohydrates and organic acids. The crude fiber is somewhat higher in the second stage, which is just previous to full ripeness. The Compass variety is conspicuously low in crude fiber, and it is very susceptible to rotting by *Sclerotinia*. In table I the data on rate of rotting show the same tendencies as were discussed in the preceding paper of this series, namely, that the resistant varieties succumb to the rot much more slowly, and when rotted have a much firmer texture than the susceptible varieties.

Conclusions

1. Plum tissue that has been rotted by *Sclerotinia cinerea* is consistently higher in ash, CaO, nitrogen, and ether extract than

is the sound tissue. This is no doubt due to loss of dry matter by respiration in the rotted samples.

2. The resistant varieties are conspicuously higher in crude fiber than the susceptible. The quality and quantity of the structural elements of the tissues no doubt are important factors in their resistance properties. The ash, nitrogen, CaO, and ether extract are lower in the resistant varieties, but not sufficiently so to constitute limiting factors in the nutrition of the invading parasite.

3. As the ripening of plums proceeds, there is a decrease in the ash, nitrogen, and calcium content, due probably to storage of carbohydrates and acids.

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"MAGNESIA INJURY" OF PLANTS GROWN IN NUTRIENT SOLUTIONS

W. F. GERICKE

Among the first signs of injury to the tops of wheat seedlings and other cereals grown in nutrient solutions of relatively high (as compared with other salts in solution) concentration of $MgSO_4$, one of the three or more salts commonly used in culture solution experimentation, is that resulting in abscission of the leaf tips of the plants. The progression of this injury consists of wilting, withering, desiccation, and finally abscission. This injury has been found to be most pronounced on young shoots. It also occurs in a much greater degree under conditions conducive for high transpiration of the plants than for low. The term "magnesia injury" has been applied to this peculiar phenomenon of abscission of leaf tips, being so named because usually found associated with comparatively high concentrations of magnesium ion (from $MgSO_4$) in nutrient solutions. Additions of soluble calcium salts to nutrient solutions giving injury were often found to be beneficial. This lent support to the concept that a certain calcium-magnesium ratio, or a range thereof, plays an important part in the physiological balance of nutrient solutions.

Recent experiments by the writer appear to bear on this magnesium question. When wheat seedlings were grown in single salt solutions it was found that some cultures gave the typical symptoms and others did not. Briefly, the tests were as follows. Seedlings 6–8 cm. high, with roots 8–10 cm. long, were fitted into and supported on paraffined corks. These were fitted into one quart containers (Mason jars) filled with the single salt solutions to be tested. The solutions were prepared from Baker's C.P. analyzed salts and distilled water. The salts were tested to see whether they conformed to specifications, but no further purification was made. A small amount of $FeSO_4$ (5 drops of 0.01 mol solution) was added to the cultures at weekly intervals. The

cultures were allowed to grow four weeks. Table I gives the experimental data.

The injury sustained by the seedlings grown in the solutions of potassium salts differed with the salts used, being least in the KH_2PO_4 set and most marked in that of K_2SO_4. Considerable abscission of the leaf tips occurred in the seedlings grown in the solutions of KNO_3, although these cultures made by far the best growth (total dry matter production) of any of the nine different salt solutions employed. In marked contrast to these are the results obtained from the cultures grown in the solutions of different calcium salts, none of which gave any symptoms of the characteristic injury. Of the cultures grown in the solutions of magnesium

TABLE I

RELATIVE EFFECTS OF SALTS IN PRODUCING ABSCISSION OF LEAF TIPS OF WHEAT SEEDLINGS

Salts	Concentration (mol)	P_H value	Injury
KNO_3	0.01	6.3	Decided
KH_2PO_4	0.01	5.2	Slight (some plants showing none)
K_2SO_4	0.01	7.4	Excessive
$Ca(NO_3)_2$	0.01	5.5	None
$CaHPO_4$ and $Ca(H_2PO_4)_2$	Saturated	5.0	None
	0.002		
$CaSO_4$	0.01	6.7	None
$Mg(NO_3)_2$	0.01	5.3	Excessive
$MgHPO_4$	0.01	6.7	None
$MgSO_4$	0.01	6.0	Excessive

salts, those grown in $Mg(NO_3)_2$ and $MgSO_4$ were severely injured, but those grown in $MgHPO_4$ were not, being perfectly normal in this respect. While the P_H values of solutions were not the same, nevertheless it is not evident that this was an important factor to account for the results.

The injury of abscission to the leaf tips of the cultures grown in the solutions of potassium salts appeared to be similar in every respect to that of the cultures grown in solutions of $Mg(NO_3)_2$ or $MgSO_4$. Whether it was physiologically the same cannot be stated at this time. If the injury to these seedlings was physiologically the same, it appears that there are at least two factors apparent in the data that are related to this injury of abscission of leaf tips, as follows:

1. The lack of or the deficiency of calcium in the nutrient media. It is in this sense that the injury to the seedlings grown in the solutions of potassium salts is to be accounted for, as it was obviously not due to the presence of magnesium. Furthermore, as the cultures grown in the different solutions of calcium salts were not injured, this is suggestive that beneficial results should obtain from additions of calcium salts to nutrient solutions that have shown themselves to be poor media for plant growth because of excessive amounts of potassium or magnesium salts. Numerous tests have proved this to be true. This, however, does not necessarily imply any definite calcium-magnesium ratio or a calcium-potassium ratio as a condition of physiological importance in nutrient solutions. The amount of calcium ions needed to overcome the harmful effects of excessive concentrations of potassium ions or magnesium ions will be determined largely by other conditions or sets of conditions under which the plants grow, of which those affecting the rate of transpiration of the plants are not of least importance.

2. The relation of phosphorus. A relatively high concentration of magnesium ion and the absence of calcium (except a trace as an impurity) in the solutions are conditions supposed to be conducive to injury. As no abscission of the leaf tips appeared in the seedlings grown in solutions of $MgHPO_4$, it appears that in the magnesium-phosphorus relation is a condition that in this case is physiologically important. It is hardly possible that the trace of calcium found in $MgHPO_4$ could account for these results. Equally large traces of calcium were found in the other salts used, especially K_2SO_4, which contained 0.005 per cent. As this amount did not prevent injury, it seems reasonable to discount the effect of a smaller trace of calcium found in $MgHPO_4$ as being the cause for the non-injury to the seedlings. The fact that KH_2PO_4 produced less injury than did any of the other potassium salts used presumably was due to some action involving the H_2PO_4 ion.

As the potassium salts and two of the magnesium salts used gave injury to the wheat seedlings, one can infer that this was due to some action of a positive ion of the salts in solution. On the other hand, certain positive ions, calcium for example, did not

produce injury. It does, as has been shown in other experiments, prevent injury where magnesium ions are excessive. The harmful effect of some of the positive ions, however, can also be prevented or greatly mitigated by the presence of certain negative ions. The phosphate ion comes in this category in the cases of the $MgHPO_4$ and KH_2PO_4 in this experiment, the former salt producing no injury and the latter salt only a little. Under certain conditions, therefore, it may be expected that additions of phosphate salts should prove beneficial to nutrient solutions that are toxic due to excessive concentrations of either magnesium or potassium. This the writer has found to be the case in other experiments.

No reference has been made to the literature, as this is to be taken up later when the subject will be discussed in greater detail.

UNIVERSITY OF CALIFORNIA

CURRENT LITERATURE

BOOK REVIEWS

Morphology and cytology of fungi

DEBARY'S great treatise, indispensable as it still is to the working mycologist, has become in many respects so obsolete as to be not only unsatisfactory but even misleading in the hands of less advanced students of the fungi, and a modern, authoritative work in the English language, with the same comprehensive scope, is greatly to be desired. The volume by Dame GWYNNE-VAUGHAN[1] in large measure meets this need, so far as the groups of which it treats are concerned. Presumably another volume in the same series is forthcoming, which will complete the account.

The first part of the book, occupying thirty-four pages, is devoted to general introductory matter, applicable to the fungi as a whole. It contains definitions, a general outline of the classification adopted, and brief discussions of such topics as saprophytism, parasitism, growth reactions, and symbiosis, the last-named term used in a narrowly restrictive sense to apply only to lichens and mycorhizas. The remainder of the book is devoted to a detailed treatment by subdivisions of the particular groups specified in the title.

In the matter of systematic treatment the author has been commendably conservative for the most part, but she has not hesitated to make radical rearrangement of the currently accepted systems where the need has existed. This is strikingly shown in the treatment of the Ascomycetes. The "great group" Ascomycetes is divided into three "groups" (why not classes and subclasses?): Plectomycetes, Discomycetes, and Pyrenomycetes. Of these, the Discomycetes includes all the orders commonly recognized as included in that assemblage; the Pyrenomycetes is made to include, with appropriate reservations, the Laboulbeniales, but does not include the Erysiphales, which are placed in the primitive "group" Plectomycetes, with the Exoascales and the Plectascales. The latter order is expanded to include everything from the Endomycetaceae and the yeasts to the Terfeziaceae. The result is an arrangement simpler and more usable than that of ENGLER, which at the same time does no violence to our present admittedly very imperfect knowledge of the relationships among these primitive forms. Furthermore, it is a pleasure to see in a modern book a reversion to the earlier conception of the Archimycetes, the Oomycetes, and the Zygomycetes as three coordinate groups of the Phycomycetes, rather than an adherence to the more recent but less logical practice of placing all the lower Phycomycetes in the Oomycetes.

[1] GWYNNE-VAUGHAN, Dame HELEN, Fungi. Ascomycetes, Ustilaginales, Uredinales. Cambridge Botanical Handbooks. pp. xi+232. *figs. 196.* Cambridge. 1922.

The general discussion of each subclass is followed by a key to its orders, and of each order by a key to its families. These keys are clear and simple, and add greatly to the value of the book. After each special topic, or discussion of a family, a bibliography is appended, in which the selection of the titles has been dictated by matured judgment. The illustrations are numerous and appropriate. Many of them are crudely drawn, which detracts greatly from the appearance of the book, but they are always clear and accurate. Much consideration is given to the cytological aspect, which in view of the research interests of the author is not surprising. The frequency with which she emphasizes the points in need of further cytological investigation should prove stimulating to workers in this field.

The implication on page 47 that we must accept two nuclear fusions as the normal situation in all Ascomycetes will be regarded by many mycologists as premature. The entire subject must be carefully reinvestigated in the light of recent parallel studies on the Basidiomycetes before this can be regarded as definitely established. In this connection, the reference to clamp connections as structures which have no significance other than to facilitate the passage of food (p. 1), and as merely vegetative phenomena (p. 188), will have to be revised. Again, the statement that "in *Puccinia*, *Phragmidium*, and other Uredinales . . . . the basidia are developed in chains" seems to stress unduly the cytological conception of the basidium, just as the thought of each cell of the promycelium as a one-spored basidium, as held by other botanists, seems to place undue emphasis on morphological detail. Lacking more convincing evidence than has yet been presented, it would seem better to retain the intermediate and generally accepted view that the teleutospore cell is not a basidium, but is the cell that gives rise to one, either externally, as a promycelium, or internally. In fact, the author is not consistent in her treatment, and seems to recognize the latter view on the same pages on which she gives different interpretations.

The proofreading has been carefully done and typographical errors are few. Fig. 27*e* is a transverse, not a longitudinal section, and a few words, mainly proper names, are misspelled, all of very minor importance. The author is to be congratulated on the effective presentation of a mass of information which has heretofore been scattered and largely inaccessible to the majority of the workers in this field. She has performed an invaluable service in collating this work and in presenting it so clearly and concisely. The book is a necessity for the reference shelf of every laboratory where mycology is taught.—G. W. MARTIN.

Lichens

Miss ANNIE L. SMITH,[2] of the British Museum, is the author of a notable work on lichens, in which are considered the history of lichenology, the morphol-

[2] SMITH, ANNIE L., Lichens. 8vo. pp. xxvii+464. *figs. 165*. Cambridge University Press, England. 1921.

ogy of the lichen thallus, reproduction in lichens, and the physiology, bionomics, phylogeny, taxonomy, ecology, and economics of lichens.

The history of lichenology is treated in seven chapters, six of which follow KREMPELHUBER in the first volume of his *Geschichte und Litteratur der Lichenologie*. The seventh period extends from 1867 to the present time. Very wisely, little space is devoted to the first six periods, as much of the work of these periods was based on a wholly wrong conception of lichens, and the systematic treatment was largely very poor. In 1867 and the following year DEBARY and SCHWENDENER established the fact that what had been considered constituent parts of lichens were algae, with which the lichens were growing in symbiotic relationship, and made modern lichenology possible. For the six periods, those especially interested can refer to KREMPELHUBER'S extended treatment; but it would seem that the seventh period, which covers all of modern lichenology, might well have received more space.

Preceding the discussion of morphology proper is a chapter in which the algal host cells are treated as constituents of the lichen, under the term "gonidia," which designation, according to the belief of many botanists, should have been consigned to oblivion long since. The treatment of the relationship between the lichen and its algal host contains much information that is valuable, but unfortunately it is all based on the supposition that the lichen is a composite structure, a fungus and many individual algae, and still in some mysterious way a plant. It is the belief of a constantly increasing number of American botanists that such a confusing presentation should never be placed before the student or the botanist.

In the treatment of types of thalli, structures peculiar to lichens, cells and cell products, general nutrition, assimilation and respiration, illumination, and color, the chapters on morphology and physiology carry much that is valuable. All is colored by a phraseology which is confusing to those who believe that lichens are fungi, however, and indeed scarcely comprehensible to them, excepting a few of the older ones, who, like the reviewer, were taught to believe that the lichen should be considered both a colony and an individual.

The chapter on reproduction on the whole is excellent, and is perhaps the most up-to-date and valuable portion of the volume. The discussion takes form under such topics as types of fruits, development of reproductive organs, apogamous reproduction, stages of apothecial development, and spores and asci. The treatment of forms of reproductive organs in lichens is the first adequate presentation to appear in a text. For those of us who believe that lichens are fungi which should be treated like other fungi, and that carpologic development and structure should play a large part in taxonomic disposition, this chapter brings our data together in convenient form so far as lichens are concerned. Unfortunately, the discussion of the matter in other Ascomycetes is given separately toward the close of the chapter.

Rather closely related to the consideration of reproduction stands that of phylogeny in another chapter. This opens with a presentation regarding the algal hosts, which many would omit from a consideration of the phylogeny of lichens. Following this is a valuable treatment of the relationships between lichens and other fungi from the standpoint of evolution. The evolution of the thallus is considered next, then that of the various groups of lichens. The chapter closes with a "scheme of suggested progression in lichen structure."

The chapter on taxonomy considers first the various schemes of arrangement, following which the lichens are arranged according to the system of ZAHLBRUCKNER, as given in ENGLER and PRANTL. Then follow treatments of number and distribution of lichens, with a survey of the lichens of polar and temperate regions, and fossil lichens. Probably ZAHLBRUCKNER would modify the classification outlined fifteen years ago considerably, were he to give his present views; but it is readily conceded that no lichenist, save perhaps WAINIO, has shown so much skill and knowledge in the classification of lichens. For one who believes that lichens are dual organisms, there is no other possibility than to consider them a distinct group of plants, as is done in the volume before us. Also, as a matter of expediency, lichens may be treated separately by those who believe that they are fungi, although at the expense of failing to present adequately the many close relationships between lichens and other fungi. In any flora which covers all fungi, distribution should be made somewhat as is done in papers by the reviewer and several other American botanists.

The chapter on bionomics contains a valuable discussion of the growth and duration of lichens, the season of fruit formation, dispersal and increase, parasitism, and the diseases of lichens. Closely related to this is the chapter on ecology, which brings together for the first time a considerable portion of the material which deals with this subject. Although the research on lichen ecology is mainly pioneer work and much of it faulty, the worker in this phase of ecology must refer to the chapter, which will be bewildering to many who have concluded that lichens are fungi.

While SCHWENDENER and other Europeans have held that lichens are fungi, they have not been able to treat lichens as fungi after the method of mycology in general. This has been left to America, where the more rational treatment of these plants began to take form a generation ago and is now taught in a considerable number of institutions and believed by many teachers and other botanists. The reviewer does not relish attacking the conception of lichens held by the author of a work of great merit. The issue is unavoidable, however, and although American botanists may get much of value from the volume, it is to be hoped that students will not be taught that lichens are not plants, but yet in some mysterious way are plants, and that maturer botanists may be able to get that which is valuable from the work and not fall into the confusing phraseology regarding the nature of lichens.—BRUCE FINK.

NOTES FOR STUDENTS

Vegetation of British Guiana.—HITCHCOCK[3] has given an interesting sketch of the conditions of plant life in British Guiana, with notes on the flora. The climate shows great uniformity of temperature, the mean maximum having the narrow variation of 83° to 87° F., and the mean minimum from 74.5° to 76.5° F. The annual rainfall ranges from 150 inches in the north to 50 inches in the south, with a relatively dry period extending from August to November. Virgin forest covers the greater part of the country, showing many of the characteristics of tropical rain forest, such as stratification, abundance of lianas, buttressed trunks for the larger trees, and great luxuriance. Attention is directed to cleanness of the forest floor due to the destruction of fallen trees and branches by decay and by wood ants. This condition is also accentuated by the scanty growth of low vegetation due to the density and uniformity of the shade. Species of the forest trees are not gregarious, but are scattered here and there.

The flora shows some interesting comparisons with that of the United States. Grasses, sedges, and leguminous plants are about equally abundant in the two regions. Some families common in the United States have here few species, as Fagaceae, Cruciferae, Ranunculaceae, Rosaceae, Labiatae, Umbelliferae, and Compositae. Some familiar families are found in Guiana chiefly as trees, as Euphorbiaceae and Solanaceae. On the other hand, certain families sparsely represented in the United States are found in greatly increased numbers. Notable among these are the Araceae, Palmaceae, Piperaceae, Rubiaceae, Myrtaceae, Lauraceae, Sapotaceae, and Melastomaceae. Orchids reach their highest development on the mountains.—GEO. D. FULLER.

Soil moisture.—As a result of recent investigations, PARKER[4] presents evidence that the vapor pressure of different moisture contents, the equilibrium relations with seeds, and the freezing point depression due to solid material do not indicate different forms of soil water such as given by the dilatometer method. This would indicate that the old method of classifying soil moisture as hygroscopic, capillary, and gravitational, although open to certain objections, still remains the best available. The opposing view, presented by BOUYOUCOS, has already been noted in this journal.[5] PARKER'S experiments, however, tend to support the views of such modern authorities as RUSSELL and KEEN that all the water present in the soil is subjected to the same law over the whole experimental range, and the various constant and critical points shown by soils at varying degrees of water content are equilibrium values only, and do not indicate any break or abrupt change in the physical condition of the soil moisture.

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[3] HITCHCOCK, A. S., Floral aspects of British Guiana. Ann. Rept. Smithsonian Inst. for 1919. pp. 293–305. *pls. 12.* 1921.

[4] PARKER, F. W., The classification of soil moisture. Soil Science **13**:43–54. 1922.

[5] BOT. GAZ. **73**:420. 1922.

In this and in a previous paper,[6] PARKER holds that the freezing point depression for the moisture equivalent and probably also for the wilting coefficient is practically a constant for all soils. This may be taken as additional evidence that the moisture equivalent and wilting coefficient are within very considerable limits constants for all soils.—GEO. D. FULLER.

Physicochemical problems relating to soil.—Under this title[7] the Faraday Society has brought together in book form the papers presented before the Society during the general discussion of this topic at its meeting in London on May 31, 1921. The discussion is divided into five sections, and was planned to form a rather complete survey of the subject. The first section is general in nature, and consists of a survey of the whole field by RUSSELL, and a discussion of the physical properties of soils in relation to survey work by ROBINSON. The second section deals with the problems of soil moisture, with papers by KEEN, ODÉN, HOAGLAND, SHULL, and HACKETT. The third section considers the organic constituents of the soil, with papers by PAGE, ODÉN, and SALISBURY. The last two sections are concerned with colloidal properties, the adsorption phenomena of section four being discussed by FISCHER, CROWTHER, and MORRISON. The final section deals with the dispersity, flocculation, and plasticity of clays by ODÉN, COMBER, and MELLOR.

The discussion as a whole forms an important addition to soil literature, and one is impressed by the usefulness of such symposia as the Faraday Society has organized from time to time. The custom of holding such general discussions devoted to an entire survey of some field of investigation is one that might well be established among scientific societies in this country to replace the less valuable type of symposium now in vogue here.—C. A. SHULL.

Photosynthesis control in forest plants.—In investigating the conditions affecting photosynthesis in forest undergrowth, LUNDEGÅRDH,[8] using a new form of assimilation-chamber, found that with variations of carbon dioxide concentration and low light intensities both the light and the carbon dioxide supply are controlling factors. The advantages from a supply of carbon dioxide above normal appear most strongly in low intensities of light. For *Oxalis acetosella* at 0.025 of sunlight, and for *Viola tricolor* at 0.25, an approximately direct proportionality was obtained between the carbon dioxide concentration and the intensity of photosynthesis. In the forest, on account of the production of the CO_2 by the ground, the air (especially that nearest the ground) becomes rich, the CO_2 content often rising to more than twice normal. This increase, least over sandy soil and greatest over the humus of beech woods,

[6] PARKER, F. W., Methods of studying the concentration and composition of the soil solution. Soil Science **12**:209–232. 1921.

[7] Physicochemical problems relating to the soil. Trans. Faraday Soc. **17**:217–368. 1922.

[8] LUNDEGÅRDH, HENDRIK, Ecological studies in the assimilation of certain forest plants and shore plants. Svensk. Bot. Tidsk. **15**:46–95. *figs.* 9. 1921.

is an important condition for the existence of shade flora. In such plants, in order that the daily products of photosynthesis may compensate the respiration of darkness, there is required at 18° C. an average illumination of little more than 0.01 light; and in order that growth may be maintained, in the case of *Oxalis*, a minimum daily illumination of 0.25 light for somewhat more than an hour. In sun plants an equilibrium between respiration and photosynthesis is reached at about 0.025 light.—GEO. D. FULLER.

Prothallia from sex organs of Polypodium.—STEIL[9] has reported that "in an old culture of *Polypodium irioides* the sterile cells of a large number of antheridia and archegonia became vegetative like ordinary prothallial cells." No case of regeneration from the sex organs of a pteridophyte has been reported previously. The cap cell and ring cells of the antheridia produced prothallial filaments and secondary antheridia; while the cells of neck and venter of the archegonia also produced filaments and antheridia, but in no case secondary archegonia. The antheridia produced in this way reached maturity, developing actively motile sperms. It was impossible to state under what cultural conditions the cells of the sex organs regenerated, but it is suggested that the peculiar behavior was the result of unfavorable conditions which appeared in the old culture.—J. M. C.

Oxalophytes over limestone.—Recent studies by SALISBURY and TANSLEY[10] have shown that *Quercus sessiliflora*, regarded as a decided oxalophyte, occurs in the regions under consideration over limestones. Analyses, however, prove that leaching has so reduced the lime content of the surface soils that they are often really acid in their reactions, and hence the oak seedlings and the accompanying calcifugous herbaceous vegetation really develop in a non-calcareous or even in an acid soil. This adds another to the rapidly accumulating array of facts indicating how dangerous it is to assume that calcareous rocks always give rise to calcareous soils.—GEO. D. FULLER.

Stock-poisoning plants.—LAWRENCE[11] has published an account of the principal stock-poisoning plants of Oregon for the use of "the Oregon farmer or stockman." The statement is made that "the annual toll of the poisonous plants in Oregon is surprisingly heavy." It is of interest to botanists to note that the principal poisonous plants of Oregon are *Delphinium* (6 spp.), *Zygadenus* (2 spp.), *Cicuta* (3 spp.), *Lupinus* (1 sp.), *Astragalus* (1 sp.), and *Pteridium* (1 sp.).—J. M. C.

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[9] STEIL, W. N., The development of prothallia and antheridia from the sex organs of *Polypodium irioides*. Bull. Torr. Bot. Club **48**:271–277. *figs. 4.* 1921.

[10] SALISBURY, E. J., and TANSLEY, A. G., The Durmast oak-woods (*Quercela sessiliflorae*) of the Silurian and Malvernian strata near Malvern. Jour. Ecol. **9**:19–38. *pl. 1.* 1921.

[11] LAWRENCE, W. E., The principal stock-poisoning plants of Oregon. Oregon Agric. Coll. Exper. Sta. Bull. 187. pp. 42. *pls. 2. figs. 10.* 1922.

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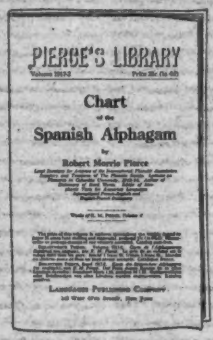

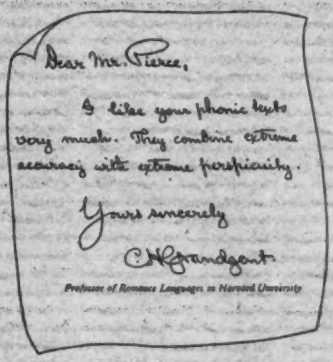
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